Genetic Improvement of the Wood Properties of *Eucalyptus nitens*

Breeding to improve solid wood and pulp properties

by

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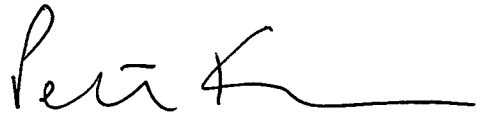
DECLARATION

This thesis does not contain any material which has been accepted for a degree or diploma by the University or any other institution. To the best of my knowledge and belief this thesis contains no material previously published or written by another person except where due acknowledgment is made in the text of this thesis.



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ABSTRACT

Eucalyptus nitens is a hardwood plantation species used in cool-temperate regions of the world. It is mainly used for pulp and paper, although there is increasing interest in using this species for producing high quality appearance and structural timber products. Therefore breeding programs need to consider the requirements of different markets and breed for a variety of end-uses.

The aim of this thesis is to study the genetic control of *E. nitens* wood properties. The focus is on three different product groupings which are pulp and paper, appearance grade timber, and structural grade timber. Pulp and paper traits studied were wood density, cellulose content, fibre length and fibre coarseness; appearance grade timber traits were collapse, checking and decay; and structural grade timber traits were stiffness and microfibril angle.

Genetic parameters and potential genetic gains were estimated using data from 12 year old *E. nitens* progeny trials grown on three sites. Wood properties were sampled using 12 mm cores taken at a height of approximately 1 metre. Relationships between whole tree wood density and core wood density, and whole tree pulp yield and core cellulose content were investigated. For both traits core samples were good predictors of whole tree values. Methods were developed to assess wood collapse and decay using wood cores.

All wood properties except fibre coarseness had significant genetic variation, with heritabilities ranging from 0.38 to 0.56. The heritability for stem diameter was 0.39. Genetic correlations between traits were mostly significant and reasonably high. Adverse correlations occurred between diameter and density, diameter and collapse, diameter and stiffness, and between density and cellulose. Favourable correlations occurred between diameter and cellulose, density and collapse and between density and stiffness. Genotype by environment interactions were sometimes present but were always small.

Genetic selection can significantly improve the quality of wood produced for pulp and paper, appearance grade timber and structural grade timber. Of particular importance are the potential gains in collapse (or checking) and stiffness, where genetic selection can potentially lift the quality grades of appearance and structural products. Selecting a deployment population for high decay resistance may minimise the risk of value loss on sites known to have severe decay problems. Breeding goals for all product groupings are reasonably well correlated and improved product quality can be achieved in all product groupings without the need for specialised breeds. Selecting for wood density, as well as growth rate, is a minimum requirement if high grades of timber are to be produced.

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PUBLICATIONS FROM THESIS

Refereed publications

Kube, P. D., Raymond, C. A. and Banham, P. W. (2001). Genetic parameters for diameter, basic density, cellulose content and fibre properties for *Eucalyptus nitens*. Forest Genetics 8: 285–294.

Kube, P. D. and Raymond, C. A. (2002). Predicting whole tree basic density and pulp yield using wood core samples in *Eucalyptus nitens*. Appita Journal 55: 43–48.

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Conference proceedings

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Co-authored publications

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Schimleck, L. R., Raymond, C. A., Beadle, C. L., Downes, G. M., Kube, P. D. and French, J. (2000). Applications of NIR spectroscopy to forest research. Appita Journal 53: 458–464.

Schimleck, L. R., Kube, P. D., Raymond, C. A., Michell, A. J. and French, J. (submitted). Estimation of whole tree kraft pulp yield of *Eucalyptus nitens* using near infrared spectra collected from increment cores. Canadian Journal of Forest Research

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CHAPTER 1

1. Introduction

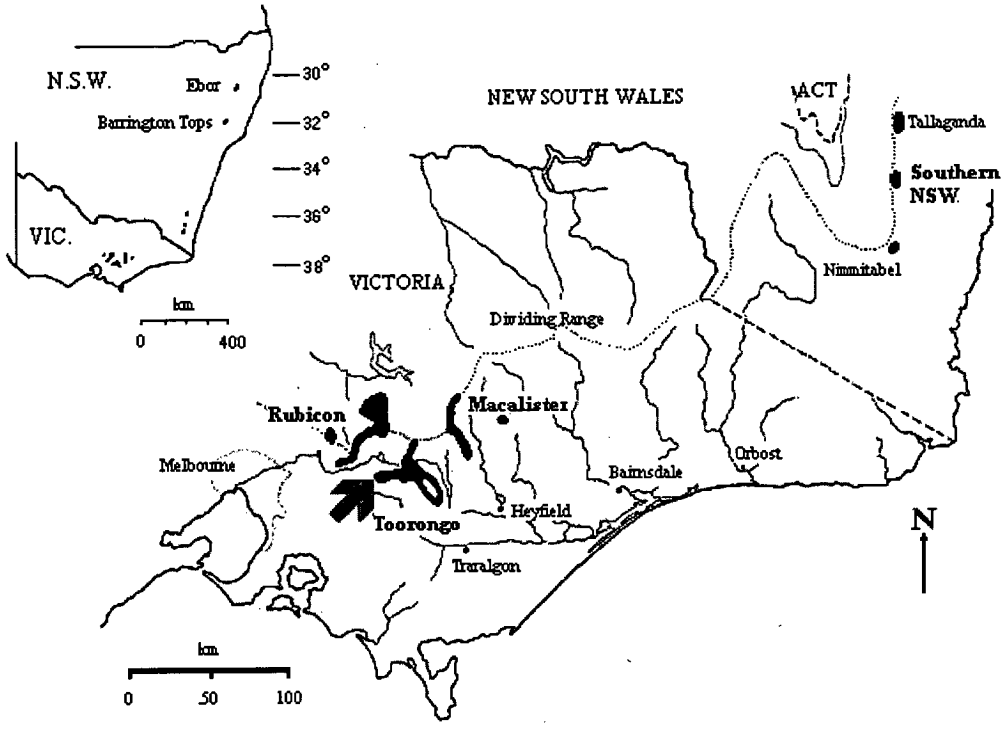
1.1 *E. NITENS* AS A PLANTATION SPECIES

Eucalyptus nitens (Deane & Maiden) Maiden naturally occurs in the higher regions of south-eastern Australia (Pederick 1979; Eldridge *et al.* 1993). It is relatively uncommon, and has a disjointed natural distribution extending from 38°S in central Victoria to 30°S in northern New South Wales (Figure 1.1). The altitudinal range is from approximately 670 m to 1280 m in Victoria and to almost 1600 m in northern New South Wales. Over the natural range the climate is cool, with occasional snowfalls and frequent frosts. Mean annual rainfall is between 750 and 1750 mm and in Victoria rainfall tends to be heavier in winter whereas in New South Wales rainfall is heavier in summer.

E. nitens is used as a hardwood plantation species in cool-temperate regions of the world. It is a preferred plantation species in these regions because of its fast growth and cold hardiness (Eldridge *et al.* 1993). Commercial plantations of this species were first established in the early 1980's, and by 1999 the global plantation area was estimated to be approximately 220,000 ha (Tibbits *et al.* 1997). The main plantation areas are in Chile (with 45% of the total area), Australia (30%), South Africa (17%) and New Zealand (5%). Plantation areas receiving their main rainfall in the winter tend to favour Victorian provenances, whereas those with a summer maximum usually use New South Wales provenances (Eldridge *et al.* 1993).

Most *E. nitens* plantations established to date are intended as short rotation crops to supply the pulp and paper industry (Tibbits *et al.* 1997). However, there is increasing interest in growing this species for the production of solid wood products. In the early 1990's programs began in Tasmania (Australia) to grow *E. nitens* for veneer, appearance and structural products as well as pulpwood (Farmer and Smith 1997, Neilsen and Pinkard 2000). These programs were driven by the reduced supply of native forest hardwoods resulting in new opportunities for plantation hardwoods. Importantly, the best market opportunities for these new plantation products are perceived to be for higher grades of timber (Beall 2000, Klemarewski *et al.* 2000).

Figure 1.1. The natural distribution of *E. nitens* (after Pederick 1979). The map shows the provenances as defined by Pederick (1979) and the arrow (↗) shows the location of the Toorongo Plateau population which was the source of material for this study.



E. nitens wood is considered well suited to the pulp and paper industry. The properties important to the profitability of kraft pulp production have been well studied and have been identified as stand growth rate, wood density and kraft pulp yield (Greaves *et al.* 1997a). *E. nitens* has good growth rates (e.g. Miller *et al.* 1992, Kiblewhite *et al.* 1998, Beadle *et al.* 1996) and the wood density and pulp yield are generally considered to be reasonably good when compared to other eucalypt species (Miller *et al.* 1992, Beadle *et al.* 1996, Clarke 2000). *E. globulus* is widely recognised as having better wood properties for kraft pulping (e.g. Beadle *et al.* 1996) but *E. nitens* is preferred on some plantation sites due to superior cold tolerance and *Mycosphaerella* resistance. The fibre qualities required for paper making are complex with some paper properties, such as strength, requiring thin walled fibres whilst others, such as optical properties, require the opposite (Arbuthnot 1991, Kibblewhite *et al.* 1998). However, *E. nitens* pulp is considered to have favourable fibre properties for paper making and is particularly well suited to the production of speciality papers (Cotterill and Macrae 1997, Kibblewhite *et al.* 1998, Kibblewhite and McKenzie 1999, Clarke 2000).

E. nitens wood also has many of the characteristics required for high quality appearance and structural products. However, there are some important and significant limitations. Saw milling trials of *E. nitens* found the main causes of downgrade in product quality were knots, checking after drying (which is the appearance of small cracks), and low strength (McKimm *et al.* 1988, Waugh and Yang 1994, Yang and Waugh 1996b, McKenzie *et al.* 2002a). Knots are a problem in *E. nitens* because this species retains dead branches. Pruning regimes have been developed to address this problem (Neilsen and Pinkard 2000) but this has been found to increase the risk of decay which can be a major risk to product quality and therefore plantation profitability (Wardlaw and Neilsen 1999, Mohammed *et al.* 2000). High levels of growth stress, which cause log splitting and deflection during sawing, are frequently identified as an important limitation for eucalypt species (e.g. Hillis 1978), but it is not clear how important growth stresses are for *E. nitens*. The saw milling studies of Waugh and Yang (1994) did not find growth stresses a problem and anecdotal evidence from Tasmania has supported this finding.[i] However, a saw milling study of *E. nitens* in New Zealand found growth stresses to be a problem in some trees (McKenzie 2002a).

Silvicultural management regimes have been developed for *E. nitens* to produce solid wood products. These regimes use pruning and thinning to grow logs of suitable dimensions, to overcome limitations caused by knots, and to minimise the risk of wood decay (Medhurst and Beadle 2000, Neilsen and Pinkard 2000). However, there appears little that can be done silviculturally to manage problems inherent with the wood properties of this species, such as checking and low strength, and tree breeding is often suggested as a tool to overcome these problems (e.g. Chafe *et al.* 1992, Evans and Ilic 2001). Tree breeding is also suggested as a means of improving other wood properties that may not be limiting, but are expected to influence product value. Raymond (2000) lists 20 attributes that are expected to be important for solid timber products (such as density variation, wood colour, and dimensional stability) but states that there is a limited knowledge about the precise requirements for these traits. Clearly, the breeding objectives for solid wood products will evolve as specific knowledge about product requirements grows.

1.2 HISTORY OF *E. NITENS* TREE IMPROVEMENT

Temperate eucalypt breeding programs commenced in the late 1960's and early 1970's and all species, including *E. nitens*, appear to have had a similar genesis. The initial emphasis was on provenance testing (Pederick 1979), followed by family tests and the assessment of genetic parameters (King and Wilcox 1988,

[i] Based on the author's observations and discussions with industry representatives.

Woolaston *et al.* 1991, Whiteman *et al.* 1992, Tibbits and Hodge 1998). In the late 1980's intensive and well planned breeding of temperate eucalypts commenced (Raymond and Volker 1989, Eldridge *et al.* 1993, Tibbits *et al.* 1997). Initially, the objectives of programs were to improve growth rates but, as programs developed, an emphasis was placed on improving the wood quality for pulp production. The traits considered important were generally growth rate and wood density. For some programs an emphasis was placed on improving pulp yield, fibre quality and fitness traits, such as frost resistance or disease resistance (Tibbits *et al.* 1997).

There has been very little effort in breeding *E. nitens* (or any other eucalypt species) for the production of solid wood products. This remains a key research issue in the development of eucalypt plantations for the production of high quality solid wood products. It is a complex issue because solid wood plantations are grown to produce a variety of products, such as appearance grade products, structural products, and pulpwood products. Therefore there is a need to understand the genetic requirements of all major product groups and how they interrelate.

1.3 SCOPE OF THIS THESIS

The aim of this thesis was to study the genetic control of the wood properties of *E. nitens*. It differs from previous work on *E. nitens* in recognising the need to breed for different product groupings. Breeding for different product groupings is based upon the premise that the grower (or industry) will wish to have the flexibility to produce a variety of products from plantations. For this thesis, three main product groupings were examined and these were appearance products, structural products, and pulpwood. Other product groupings are recognised (such as natural round wood, and reconstituted products) but these are not considered here.

Appearance grade products are used in applications where the visual characteristics of the product are of prime importance. The main market sectors include high-value furniture, joinery, panelling, flooring and veneers (Hillis 2000). A key requirement for these products is the absence of imperfections, such as checking, decay, discoloration and knots. Structural grade products are used in engineering applications and the primarily requirements are stiffness and strength (Hillis 2000). The main market sector is framing and formwork in buildings. Pulpwood is used as a source of pulp for paper making. The main market sectors include chemical pulp, where fibres are separated by chemical digestion, and mechanical pulp, where fibres are separated by mechanical grinding (Smook 1982).

Key traits for each of the major product groupings were identified from reported utilisation studies of *E. nitens* (e.g. Yang and Waugh 1996b, Greaves *et al.* 1997a, McKenzie *et al.* 2002a), discussions with wood science researchers and industry people (e.g. Raymond 2000), and experiences with silvicultural studies (e.g. Wardlaw and Neilsen 1999). This work does not purport to be a complete study of this very broad topic, but instead has selected what are currently thought to be some of the most important traits. These are used to begin examining how breeding might be done for different product groups.

Chapter 2 presents studies of methodologies by which trees can be sampled for wood density and pulp yield. Traditional methods of assessing pulp yield have been slow, destructive and expensive and this has limited potential genetic gains. Therefore in this chapter non-destructive and low cost methods to assess these wood properties are developed. Such techniques allow large numbers of trees to be assessed, and allow sampled trees to be used for ongoing breeding. This maximises genetic gains and minimises the costs of breeding programs. For wood density, the relationship between whole tree density and the basic density of a 12 mm diameter bark to bark wood core taken from near breast height was evaluated. For pulp yield, the relationship between whole tree pulp yield and the cellulose content of a wood core was evaluated.

Chapter 3 presents a study of the genetic control of traits important for wood fibre production. These traits were stem diameter, wood density, cellulose content, fibre length, and fibre coarseness. A major aim was to estimate the genetic gains that could be achieved using the low cost and non-destructive sampling techniques developed in Chapter 2. Genetic parameters and genotype by environment interactions were also estimated. Genetic parameters are required to develop breeding strategies, estimate breeding values, and to determine gains from selection (Falconer 1993). Genotype by environment interactions measure the stability of genotypes across environments and, if present, indicate that the best genotype in one environment may not be the best in another (Falconer 1993).

Chapter 4 presents a study of the genetic control of collapse and checking. Checking has been identified as the major cause of downgrade for appearance grade products. Checking occurs during drying and refers to small cracks that form in the timber. Collapse, which refers to the buckling of cell walls during drying, is recognised as a major cause of checking and was used as an indicator of checking potential. The main aim of this chapter was to evaluate tree breeding as a means of managing these problems. In addition, genetic parameters and genotype by environment interactions for collapse were assessed, and relationships between collapse and traits important to a pulpwood breeding objective evaluated.

Chapter 5 presents a study of the genetic control of wood decay. Wood decay is a major risk to the profitability of plantations grown for appearance products. Decay is associated with pruning and thinning wounds that occur with the silvicultural management of these plantations. The aim of this chapter was to evaluate tree breeding as a tool to minimise the effects of wood decay. In addition, assessment and analytical techniques were evaluated, genetic parameters estimated, and relationships between wood decay and the traits important to a pulpwood breeding objective evaluated.

Chapter 6 presents a study of the genetic control of wood stiffness. Stiffness, which defines the timber bending strength under load, is a fundamental property used to define structural timber grades. It has been recognised that the stiffness of plantation grown *E. nitens* will be limiting in some markets, such as those traditionally supplied by eucalypts harvested from native forests. The major aims of this chapter were to investigate the genetic control of stiffness, estimate the genetic gains that can potentially be made, and to explore options for selecting for stiffness in breeding programs. In addition, genetic parameters for stiffness and microfibril angle were estimated, and relationships between stiffness and traits important to a pulpwood breeding objective evaluated.

Chapter 7 presents studies of different selection strategies for the genetic improvement of wood density. Wood density is a fundamental trait to all product groupings (that is, pulpwood, appearance products and structural products). It is not practical to sample every tree for wood density in a breeding program and therefore there is a need to determine the best sampling strategy. The aim of this chapter was to evaluate different sampling strategies. An additional aim was to compare genetic gains obtained using an instrument called a Pilodyn with those obtained by taking wood cores. A Pilodyn measures wood density indirectly by measuring the depth of penetration of a flat nosed pin when driven into a wood sample with a fixed force. Some studies have found this to be a simple and very low cost method to assess wood density (e.g. Greaves *et al.* 1996).

The data used in this thesis is all derived from a single set of progeny trials. These trials consist of open pollinated progeny of 40 native forest families from the Toorongo Plateau in the central highlands of Victoria. The location of this population is shown in Figure 1.1 and more details about the trials are given in the following chapters. Data was collected for a total of 19 different traits and the aim was to measure traits important for each product grouping (that is, pulpwood, appearance products and structural products) on the same trees. A summary of all traits measured and of the datasets used in each chapter is given in Table 1.1. For some traits, such as diameter and wood density, the same data is used in different chapters so that relationships between traits could be presented. These trials were grown under a pulpwood silvicultural regime (with no thinning) rather than a

sawlog regime (which would involve at least one thinning). This may influence the appearance grade and structural grade traits, although very little is known about the silvicultural stocking affects these wood properties.

Table 1.1. Summary of traits studied in this thesis, age at which measurements were made and chapters in which data is presented.

Trait		Age (years)	Number of sites	Chapters in which data is used
D_6	Stem diameter (cm)	6	3	3
D_{12}	Stem diameter (cm)	12	3	3, 4, 5, 6, 7
D_{INC}	Diameter increment (cm)	6 - 12	3	3
BD	Basic density, core (kg m^{-3})	12	3	3, 4, 5, 6, 7
CEL	Cellulose, core (% kg kg^{-1})	13	3	3, 4, 5, 6
FL	Fibre length, core (μm)	12	3	3
FC	Fibre coarseness, core (μg m^{-1})	12	3	3
COL	Tangential collapse (%)	12	3	4
EXT	Ethanol soluble extractives (%)	13	3	5
BR	Branch score (1 to 6)	6	2	5
DEC_h	Incidence of heart-rot decay	13	2	5
DEC_w	Incidence of wounding decay	13	1	5
DIC_h	Incidence of heart-rot discolouration	13	2	5
DIC_w	Incidence of wound discolouration	13	1	5
AD_{silvi}	Silviscan-2 air dried density (kg m^{-3})	10	1	6
MFA	Silviscan-2 microfibril angle (°)	10	1	6
MOE	Silviscan-2 modulus of elasticity (GPa)	10	1	6
PD_S	Pilodyn penetration, summer (mm)	13	3	7
PD_W	Pilodyn penetration, winter (mm)	14	3	7

CHAPTER 2

2. Predicting Whole Tree Basic Density and Pulp Yield Using Wood Core Samples [ii]

2.1 INTRODUCTION

The profitability of kraft pulp production is influenced by wood density and pulp yield (Borralho *et al.* 1993, Dean *et al.* 1990, Greaves *et al.* 1997a). Tree breeding programs aim to improve profitability by changing these wood properties. Breeding programs require a large number of samples to be screened using non-destructive sampling techniques to preserve valuable genetic material. Therefore small samples need to be taken from a representative and accessible part of the tree in a cost-effective manner.

Assessment of wood properties using cores at breast height is a commonly used technique (Zobel and Jett 1995). However, wood properties of a core are often different to whole tree averages. Therefore it is necessary to test the strength of relationships between core values and whole tree values, and to define these relationships so sample data can be converted to whole-tree, or whole-crop values.

Relationships between core density and whole tree density have been defined for a number of eucalypts. High correlations have been found between density of cores and whole tree density for *E. grandis* (Ferreira 1972, Barrichelo *et al.* 1983, Vital and della Lucia 1987) and *E. globulus* (Raymond and Muneri 2001). For *E. nitens*, high correlations were found on a single New Zealand site (Lausberg *et al.* 1995) but across a range of Australian sites correlations were found to be variable, with some sites having weak and atypical relationships (Raymond and Muneri 2001). The latter study recommended that a destructive sampling program be undertaken for *E. nitens* prior to major core sampling programs.

Pulp yield of individual trees has traditionally been assessed by cooking wood chips in an alkaline solution at elevated temperature and pressure in a laboratory digester (Smook 1982). This method requires a relatively large quantity of wood chips and sample trees must be felled, sectioned and chipped. This process

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destroys the tree and therefore it is not available for future breeding work unless grafted prior to falling. It is also slow and costly and, consequently, not well suited to screening a large number of samples. Attempts have been made to seek more cost effective methods by examining potential secondary standards, such as components of wood chemical composition, which will correlate strongly with pulp yield. Properties examined include extractives, lignin, and cellulose (Zobel and Jett 1995, Turner *et al.* 1983, Raymond *et al.* 1994, Wallis *et al.* 1996).

Cellulose content is positively correlated with pulp yield and appears to have been the most reliable indicator of pulp yield for plantation eucalypts. Strong relationships between cellulose content and pulp yield were found for *E. globulus* (Dillner *et al.* 1971, Wallis *et al.* 1996), *E. grandis* (duPlooy 1980) and *E. nitens* (Wallis *et al.* 1996). These studies all used disc samples from at least two points in the stem or billets.

Extractives content tends to be negatively correlated with pulp yield. Some studies have found strong relationships between extractives and pulp yield (Turner *et al.* 1983, Wallis *et al.* 1996) but in other studies this relationship has been weak (Raymond *et al.* 1994). The relationship is based on the premise that wood with a high mass of extractives has a lower mass of kraft pulp since the extractives are a component removed during pulping. Relationships are generally evident when there are large differences in extractives content, but when differences are small relationships are weak. In the study of Raymond *et al.* (1994) the relationship was weak over the range of pulp yields and extractive contents encountered when age, species and sites did not vary.

Use of cellulose assays has been hindered by unreliable results, cumbersome methodology and safety considerations (Zobel and Jett 1995, Wallis *et al.* 1997). Cellulose content can be determined using a number of methods with varying degrees of accuracy. Techniques used include a peroxyacetic acid method (Garbutt 1989), a nitric-acetic acid method (Pereira 1988) and a dioxane-acetylacetone-hydrochloric acid method (Seifert 1960). A comparison of these methods (Wallis *et al.* 1997) indicated differing results with various levels of impurities present in the different methods. Each method relies on refluxing samples for between twenty-five minutes and three hours, restricting the numbers of samples that could be processed. In addition, a variety of solvents were used with varying degrees of toxicity. The Seifert technique was found to give the most accurate cellulose values and produced the purest cellulose residues (Wallis *et al.* 1997). However, the solvent mixture (acetylacetone-dioxane-hydrochloric acid) used to digest the wood has problems as acetylacetone is a reactive solvent and dioxane has toxic properties. Due to these problems a new technique was developed using less toxic chemicals (Wallis *et al.* 1997). It is based on an acid-diglyme digestion which can be undertaken in a sealed bottle allowing multiple

samples to be processed simultaneously. This method has overcome most problems although there are some concerns about the safety of diglyme.

The aims of this study were to evaluate methods and develop relationships for predicting whole tree basic density and pulp yield from core samples of 12 year-old *E. nitens* in Tasmania. There were three main aspects to this study. Firstly, longitudinal patterns of variation in basic density, cellulose content and extractives content were determined; secondly, the correlations between cores and whole tree values for basic density, cellulose content and extractives content were assessed; and thirdly, relationships between whole tree pulp yield, cellulose content and methanol soluble extractives content were calculated.

2.2 MATERIALS AND METHODS

2.2.1 Basic density

Ten trees from each of three sites in northern Tasmania were sampled (Table 2.1). The sites were progeny tests containing trees raised from open pollinated seed from 40 native forest families originating from the Toorongo Plateau in the central highlands of Victoria. Samples were taken at age 12 years and trees were selected to cover the range of diameter classes. Mean diameters, heights and basic densities of sample trees are summarised in Table 2.2. Two years later (at age 14 years) an additional 25 trees were sampled for basic density from the Gog site. These were sampled as part of the pulp testing program (see section 2.2.2).

Table 2.1. Description of field sites.

	Dial	Gog	Kamona
Latitude (South)	41° 10'	41° 29'	41° 08'
Longitude (East)	146° 04'	146° 23'	147° 40'
Altitude (m)	100	300	160
Rainfall (mm/year)	1060	1200	1150
Mean maximum temp. warmest month (°C)	22.3	21.8	23.4
Mean minimum temp. coolest month (°C)	3.8	2.4	2.5
Parent material	mudstone	Basalt	granite

Sample trees were felled and 25-mm thick discs taken from 0, 10, 20, 30, 40, 50, 60, and 70% of total height. A fixed-height sample was taken at 0.9 m, which is the sampling height recommended by Raymond and Muneri (2001), and a 15-mm bark-to-bark strip was cut from this disc to simulate a core. Green volumes for all discs and cores were measured using the water displacement method (Hendrichs and Lassen 1970) and basic density calculated after drying at 105°C until a constant weight was reached (about 3 days for discs). Under-bark diameters were measured on discs and used to calculate tree volume. Whole-tree density was calculated by using disc densities to apply an appropriate weighting longitudinally

obtain the stem. Whole-tree basic density was also measured using wood chips for trees sampled for pulp testing. Discs were chipped using a laboratory chipper and volume was measured on a subset of chips after a seven-day soak in water to reach maximum moisture content.

Table 2.2. Summary statistics for sampled trees, with standard deviation in brackets. Wood properties are whole tree values.

	Dial age 12	Gog age 12	Kamona Age 12	Gog age 14
Sample size	10	10	10	25
Mean dbh (cm)	21.4 (3.7)	23.5 (2.7)	24.6 (5.2)	23.6 (3.8)
Mean height (m)	20.3 (1.8)	20.7 (2.0)	21.9 (2.0)	21.2 (2.5)
Basic density (kg/m^3)	467 (25)	478 (29)	480 (45)	508 (39)
Pulp yield (%)	-	-	-	53.3 (1.9)
Cellulose (%)	-	-	-	42.0 (1.7)
Extractives (%)	-	-	-	3.0 (0.8)

Linear relationships between core density and whole tree density were calculated for each site separately. The significance of differences between regression coefficients was tested to see if there were different relationships at different sites. The significance of differences in longitudinal density profiles were assessed by fitting the following linear model using analysis of variance:

$$Y_{ij} = \mu + S_i + H_j + S.H_{ij} + \varepsilon \qquad (2.1)$$

where Y_{ij} is the disc density, μ is the overall mean, S_i the effect of the ith site, H_j the effect of the jth percentage height, $S.H_{ij}$ the interaction between the ith site and jth percentage height, and ε the random error.

2.2.2 Pulp yield

Pulp yield samples were taken from the Gog site. In another study (Chapter 3 of this thesis), 186 trees at this site were core sampled and assessed for basic density and cellulose content. Twenty-five trees were chosen to cover the full range of basic density and cellulose contents and harvested at age 14 for pulp yield determination. Sample trees were felled and 25-mm discs taken at 0, 10, 20, 30, 40, 50, 60, and 70% of total height. Details of sample trees are given in Table 2.2.

Pulp testing was done by the Fibre Technology Division of Gunns Ltd.[iii] Discs were chipped using a laboratory mini-chipper and all chips for each tree mixed. Each tree was individually pulped using a Haato 12 autoclave air pulping digester. Between 2 and 3 tests were done for each tree. Samples were tested under the

[iii] Fibre Technology, Gunns Ltd., locked bag 25 Burnie, Tasmania, 7320, Australia. This is a commercial wood testing laboratory which routinely tests wood samples for Kraft pulp yield.

following conditions: wood charge 300 g o.d.; sulphidity 25%; time to and time at temperature, 90 and 90 minutes; cook temperature 170°C, liquor ratio 3.5 to 1, H factor 2865; and % alkali variable to give kappa 18. Pulp yield at kappa 18 was estimated for each tree using standard response curves.

2.2.3 Cellulose content

Wood core samples for cellulose analysis were taken at a height of 0.9 m at age 12 years using a 12-mm diameter bark-to-bark core. In addition, discs were taken from 0, 20, 40 and 60% of total height when trees were felled for pulp testing. Cores were first reduced to small fragments using a 200-mm disc pulveriser and then reduced to wood meal in a Wiley Mill with a 1-mm screen. For the discs, wood shavings were collected using a drill press with a 7-mm drill bit, dried at 27°C and ground in a Wiley mill. All 25 trees had cellulose contents measured for cores and 12 trees had cellulose contents measured for the percentage heights. For these 12 trees, under-bark diameters and basic density were also measured.

Crude cellulose content (g cellulose per dry mass) was measured using the method of Wallis *et al.* (1997). Non-cellulosic compounds were solubilized by digestion in diglyme and hydrochloric acid in a sealed bottle for one hour on a shaker table in a water bath at 90°C. The residue was collected by filtration, washed, dried and weighed to determine crude cellulose mass. Duplicate samples were assayed for all cores, and 25% of percentage height samples as a general check on accuracy.

Whole-tree cellulose content was calculated using volume and density measurements. Correlations and linear relationships between core cellulose content, whole tree cellulose content, and whole tree pulp yield were then calculated. The significance of differences in cellulose content for longitudinal profiles were tested using analysis of variance to fit the following linear model:

$$Y_{jk} = \mu + H_j + T_k + \varepsilon \qquad (2.2)$$

where Y_{jk} is the disc cellulose content, μ is the overall mean, H_j the effect of the jth percentage height, T_k the effect of the kth tree, and ε the random error.

2.2.4 Extractives content

Methanol-soluble extractives content was measured on 18 of the 25 trees felled for pulp testing. Samples were taken from 0, 20, 40 and 60% of total height, and a bark to bark strip was cut from a disc at 0.9 m to simulate a core. Wood meal was prepared using the same method as that used for the cellulose assay.

A Soxhlet extractor was used to remove the methanol-soluble extractives from the wood meal. Approximately 2.5 g of wood was used. The extraction process was allowed to run until the solvent ran clear, and this took between two and four hours. The weight loss of the wood sample was measured and, using volume and

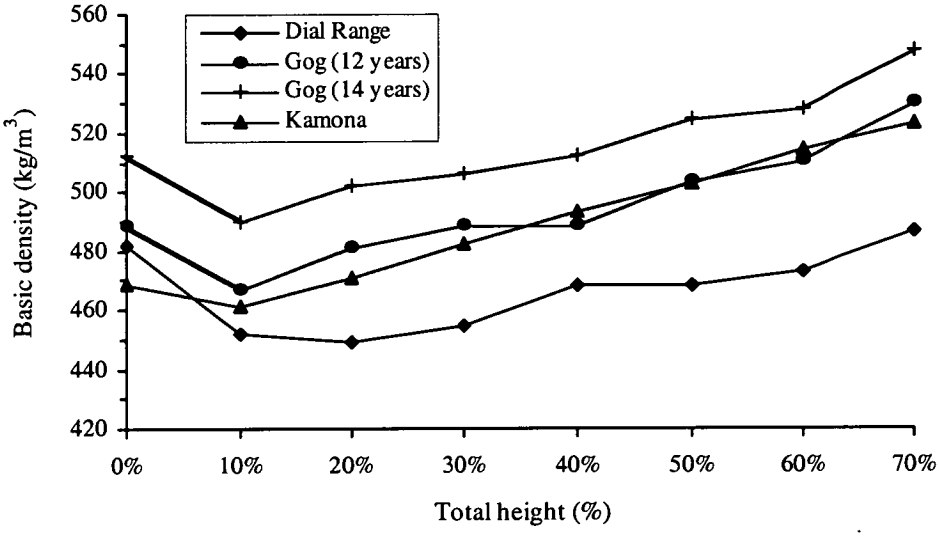
density measurements, whole tree extractives content calculated. The significance of differences in extractives content in longitudinal profiles were tested using the same linear model as that used for cellulose content.

2.3 RESULTS AND DISCUSSION

2.3.1 Basic density

Basic density was significantly different at different sampling heights ($P<0.001$) and the pattern of variation was similar across all sites (Figure 2.1). Density decreased between the stump and 10% of height (about 2.5 m), where it was at a minimum, and then increased in a linear pattern to a maximum at 70% height. This pattern is identical to that previously reported for this species (Raymond and Muneri 2001, Raymond and MacDonald 1998).

Figure 2.1. Pattern of longitudinal variation in basic density for each site.



Patterns of variation were broadly similar across sites (Figure 2.1), but there were statistically significant interactions ($P=0.01$) between site and density at 0 and 10% of tree height. All sites differed in the rate of change between 0 and 10% height. Dial had the most rapid rate of change, Kamona had the lowest rate of change, and Gog (at both sampling ages) had an intermediate rate of change. These patterns were consistent within sites, although Raymond and Muneri (2001) report results which suggest these patterns sometimes vary within sites. Patterns of variation between 20% and 70% height were consistent across sites, and there were no significant site by height interaction effects in this range.

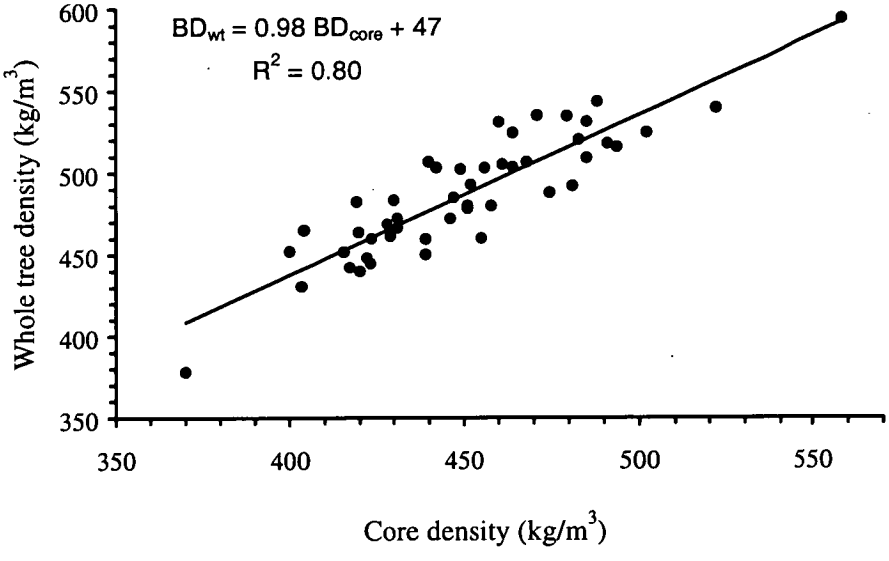
Whole-tree basic density can be reliably predicted from a core taken at 0.9 m. Cores explained between 85% and 92% of variation in whole tree density when

sites were kept separate and 80% of variation when all sites were combined (Table 2.3 and Figure 2.2). Relationships between core density and whole-tree density varied slightly between sites (Table 2.3) but differences were not statistically significant (at P=0.05). Over the range of expected values the equations in Table 2.3 are very similar and differences in predicted density when using a local model instead of a global model were no more than 1%. Furthermore, the relationship between core density and whole tree density developed from this data is not significantly different to that reported by Raymond and Muneri (2001) for *E. nitens* aged between 7 and 9 years. Therefore it appears that within-tree patterns of variation are consistent across ages and sites, and a single global relationship can be used to predict whole tree density for the range of sites covered in these two studies.

Table 2.3. Equations to predict whole tree basic density (BD_{wt} in kg m^{-3}) and whole tree chip basic density (BD_{chip} in kg m^{-3}) from basic density of a core at 0.9 m height (BD_{core} in kg m^{-3}), plus 95% confidence intervals for coefficients in brackets).

Dial	BD_{wt}	=	BD_{core}	*	0.81 (±0.20)	+	113 (±88)	$R^2 = 0.92$	n = 10
Gog-12	BD_{wt}	=	BD_{core}	*	0.91 (±0.31)	+	63 (±140)	$R^2 = 0.85$	n = 10
Gog-14	BD_{wt}	=	BD_{core}	*	0.85 (±0.17)	+	119 (±78)	$R^2 = 0.88$	n = 18
Kamona	BD_{wt}	=	BD_{core}	*	1.05 (±0.29)	+	15 (±129)	$R^2 = 0.92$	n = 10
All sites	BD_{wt}	=	BD_{core}	*	0.98 (±0.15)	+	47 (±66)	$R^2 = 0.80$	n = 48
Gog-14	BD_{chip}	=	BD_{core}	*	0.76 (±0.20)	+	166 (±91)	$R^2 = 0.81$	n = 18

Figure 2.2. Relationship between basic density of a core at 0.9 m and whole tree basic density across all sites.



2.3.2 Cellulose content

Cellulose content was significantly different ($P<0.001$) at different sampling heights (Figure 2.3). The pattern of variation was parabolic, with a maximum value at about 20% of tree height (about 5 m). At this height, average cellulose content was 2% higher than that at stump height. Cellulose contents at stump height and 60% height (15 m) were almost identical. All trees showed a similar pattern of longitudinal variation, although the difference between the maximum value and minimum value ranged from 1.3 to 3.8%. The cellulose content at any point in the stem could be explained by the equation:

$$CEL_{ht} = 36.98\ HT^3 - 54.90\ HT^2 + 19.79\ HT + 40.62 \qquad R^2 = 1$$

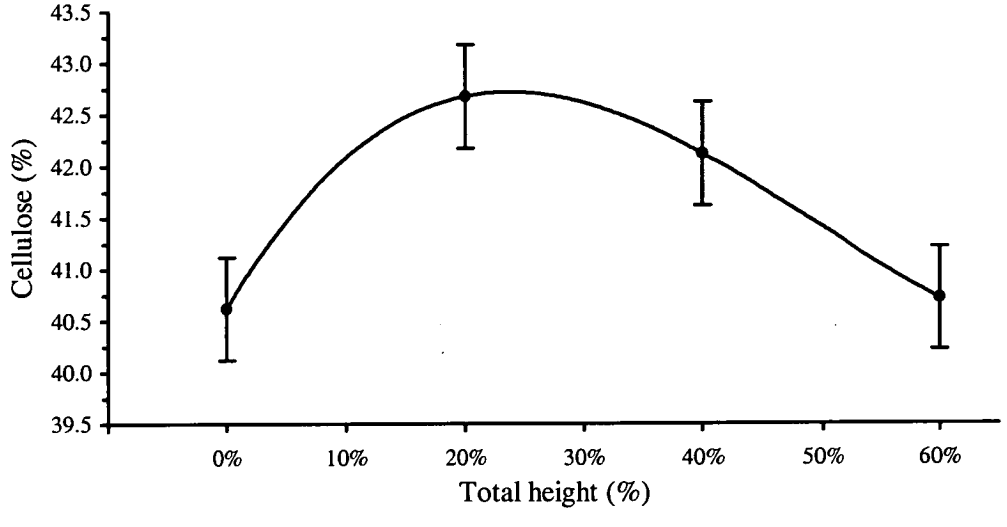
where CEL_{ht} is the percentage cellulose content of a disc at a given height (kg/kg) and HT is the stem height as a proportion of total height.

Whole-tree cellulose content can be reliably predicted using the cellulose content from a core taken at 0.9 m with 89% of the variation in whole-tree cellulose being explained by core data. The relationship can be described using the equation:

$$CEL_{wt} = 0.821\ CEL_{core} + 8.415 \qquad R^2 = 0.89$$

where CEL_{wt} is the whole tree cellulose content (kg/kg) and CEL_{core} is the cellulose content of a core from 0.9 m. The cellulose content of a core was lower than that of discs at every height, reflecting the different sampling patterns of cores and discs. Cores samples contain relatively lower proportions of outer wood than discs and the pulp yield from outer rings can be up to 8 percentage points higher than that of the inner wood (Downes *et al.* 1997).

Figure 2.3. Pattern of longitudinal variation in cellulose content for 14 year old *E. nitens* at Gog (with standard errors). Each point is a mean of 12 values.



2.3.3 Extractives content

Extractives content was significantly different ($P<0.001$) at different sampling heights (Figure 2.4). Extractives content was highest at the stump, and decreased along the length of the stem in a non-linear fashion. All trees had a similar pattern of longitudinal variation, although the differences between the stump and 60% height varied from 1.3% to 5.3%. The extractives content at any point in the stem could be explained by the equation:

$$EXT_{ht} = 10.67\ HT^2 + 11.23\ HT + 5.07 \qquad R^2 = 0.96$$

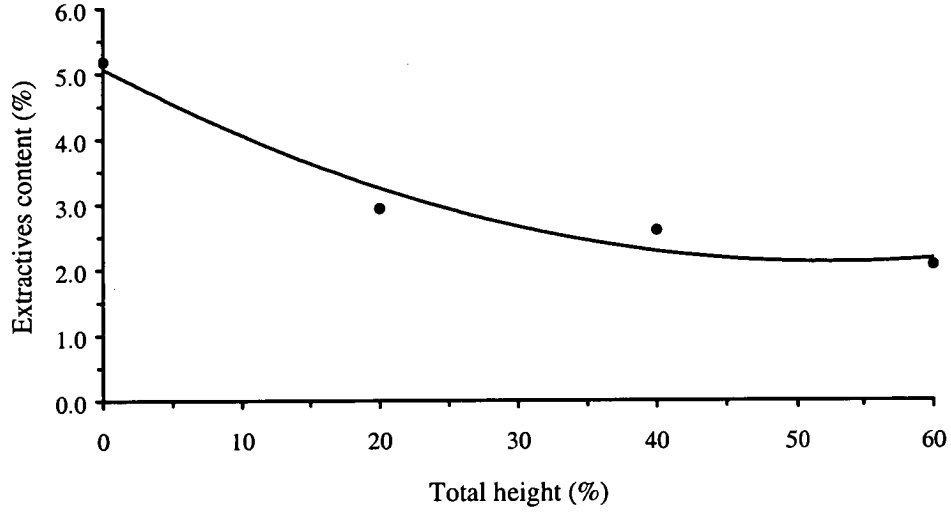
where EXT_{ht} is the percentage methanol soluble extractives content of a disc at a given height (kg/kg) and HT is the stem height as a proportion of total height.

Whole tree extractives content can be predicted from the extractives content of a core. However, the relationship is not as strong as that for basic density and cellulose content with only 56% of variation in whole tree values being explained by core values. The relationship can be described by the equation:

$$EXT_{wt} = 0.790\ EXT_{core} - 4.497 \qquad R^2 = 0.56$$

where EXT_{wt} is the whole tree extractives content (kg/kg) and EXT_{core} is the extractives content of a core from 0.9 m.

Figure 2.4. Pattern of longitudinal variation in methanol soluble extractives content for 14 year old *E. nitens* at Gog (each point is a mean of 18 values).



2.3.4 Predicting pulp yield

Correlations between pulp yield, basic density, cellulose content and extractives content are shown in Table 2.4. Relationships between cellulose content and pulp yield were significant and strong. Relationships between extractives content and pulp yield were also significant, but weaker. Basic density and tree diameter were not related to pulp yield.

Table 2.4. Correlation coefficients (r) between variables for age 14 trees at Gog. Abbreviations used are described below the table.

	PY_{K18}	PY	D_{12}	BD_{core}	BD_{chip}	BD_{wt}	CEL_{wt}	CEL_{core}	EXT_{wt}
PY	0.95 **								
D_{12}	0.21	0.15							
BD_{core}	-0.15	-0.11	-0.54 **						
BD_{chip}	0.03	0.05	-0.44 *	0.90 **					
BD_{wt}	-0.06	0.00	-0.66 **	0.94 **	0.96 **				
CEL_{wt}	0.89 **	0.83 **	-0.02	-0.04	0.06	-0.06			
CEL_{core}	0.83 **	0.74 **	0.33 *	-0.12	0.03	-0.11	0.90 **		
EXT_{wt}	-0.55 **	-0.44 **	0.24	-0.08	-0.12	-0.13	-0.62 *	-0.22	
EXT_{core}	-0.49 **	-0.39 *	0.09	0.10	0.03	0.08	-0.61 *	-0.31	0.75 **

** = significantly different from zero at P<0.01; * = significant at P<0.05

PY pulp yield (%) at a common chemical charge (NaOH = 17%)
PY_{K18} pulp yield (%) after correction to kappa 18
D_{12} diameter (cm) at 1.3 m at age 12
BD_{core} basic density (kg m^{-3}) of a core sample from 0.9 m height
BD_{chip} whole tree basic density (kg m^{-3})
BD_{wt} whole tree chip basic density (kg m^{-3})
CEL_{WT} percentage cellulose content of the whole tree (kg/kg)
CEL_{core} percentage cellulose content of a core at 0.9 m (kg/kg)
EXT_{wt} extractives content (%) for the whole tree
EXT_{core} extractives content (%) for a core sample from 0.9 m height

Core cellulose content is positively related to pulp yield and is a reliable predictor of whole tree pulp yield. Core cellulose content explained 68% of variation in pulp yield after correction to kappa 18 and 55% of variation of pulp yield at a common chemical charge (Figure 2.5 and Table 2.5, equations 1 and 2). Outliers in Figure 2.5 (a total of six samples) were repeated to determine if problems were due to the fundamental nature of the relationship between cellulose and pulp yield, or the assay method itself. The relationship improved substantially after repeating these samples (Table 2.5, equations 3 and 4). Core cellulose content then explained 86% of variation in pulp yield after correction to kappa 18 and 76% of variation in pulp yield at a common chemical charge.

Figure 2.5. Relationship between cellulose content of cores at 0.9 m height and whole tree pulp yield at kappa 18 for 14 year old *E. nitens* at Gog.

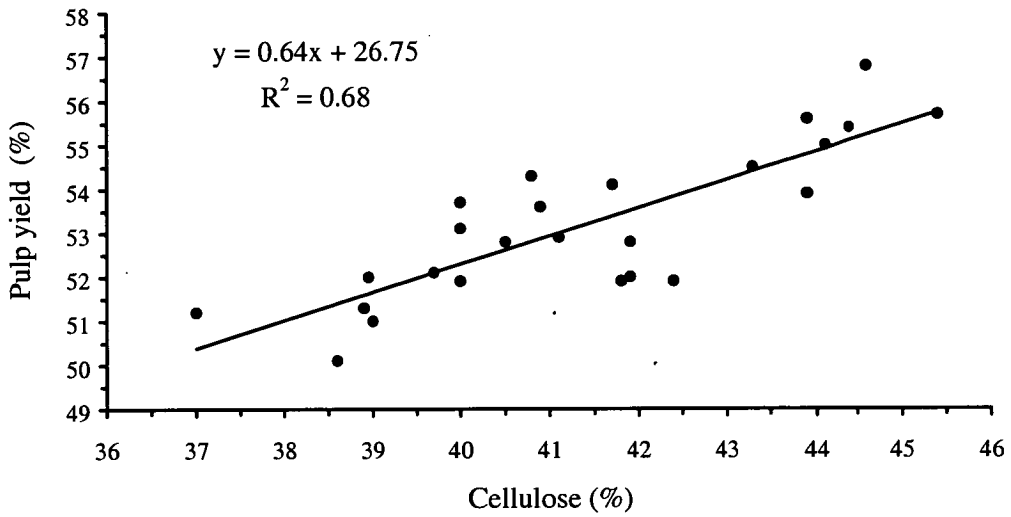


Table 2.5. Equations to predict whole tree pulp yield (%) from cellulose content (± 95% confidence intervals). Equations 1 and 2 are for original data, and equations 3 and 4 are for data after outliers were reassayed for cellulose content.

1	PY_{K18} [i]	= CEL_{core} [ii]	*	0.64 (± 0.19)	+	26.75 (± 7.80)	R^2 = 0.68	n = 25
2	PY [iii]	= CEL_{core}	*	0.39 (± 0.15)	+	37.40 (± 6.37)	R^2 = 0.55	n = 25
3	PY_{K18}	= CEL_{core}	*	0.75 (± 0.13)	+	22.74 (± 5.23)	R^2 = 0.86	n = 25
4	PY	= CEL_{core}	*	0.48 (± 0.12)	+	34.01 (± 4.72)	R^2 = 0.76	n = 25
5	PY_{K18}	= CEL_{wt} [iv]	*	1.09 (± 0.41)	+	7.58 (± 16.98)	R^2 = 0.78	n = 12
6	PY	= CEL_{wt}	*	0.67 (± 0.32)	+	25.90 (± 13.17)	R^2 = 0.69	n = 12

i) PY_{K18} is the percentage pulp yield after correction to kappa 18

ii) CEL_{core} is the percentage cellulose content of a core at 0.9 m (kg/kg)

iii) PY is the percentage pulp yield at a common chemical charge (NaOH = 17%)

iv) CEL_{wt} is the percentage cellulose content of the whole tree (kg/kg)

Extractives content is significantly and inversely related to pulp yield but does not appear to be a useful predictor of pulp yield. At best, the extractives content of a core explained only 24% of variation in pulp yield. Multi-variate relationships including cellulose and extractives contents of cores were also evaluated. Relationships improved (for example R^2 for equations 1 and 3 in Table 2.5 increased to 0.79 and 0.89 respectively), but the coefficients for extractives were not significantly different from zero (at P=0.05) and the relative contribution of extractives was very small compared to that from cellulose.

Whole-tree cellulose content explained 78% of variation in pulp yield after correction to kappa 18 and 69% of variation of pulp yield at a common chemical charge (Table 2.5). These relationships are similar to those that can be calculated using the data of Wallis *et al.* (1996), which were also based upon whole-tree

cellulose values. Relationships between cellulose content and pulp yield are different for cores and whole trees (compare equations 3 and 4 with 5 and 6). Whole-tree cellulose appears directly related to pulp yield, with a one unit gain in cellulose content resulting in an equivalent gain in pulp yield, whereas a one unit gain in core cellulose content does not translate directly to a one unit gain in pulp yield. This could be explained by the radial variation in pulp yield. Wood in outer growth rings has pulp yields approximately 10% higher than that of inner growth rings (Downes *et al.* 1997). The quantities of this higher pulp yield wood sampled in a core are lower than that in a disc, and therefore a given change in whole tree values is reflected by lower changes in a core. Given these patterns of variation, it is important when converting cellulose content to pulp yield that relationships for cores are not applied to discs or whole trees.

2.4 CONCLUSIONS

Whole-tree values for basic density, cellulose content and kraft pulp yield were all reliably predicted by core samples taken at a height of 0.9 m. For basic density, the core samples explained between 85 and 92% of variation in whole tree basic density, whilst for cellulose content cores explained 89% of variation in whole tree values.

Cellulose content of a core from 0.9 m was also a very good predictor of kraft pulp yield of the whole tree, with potentially up to 86% of the variation in yield at kappa 18 accounted from by the core sample. However, this level of accuracy is unlikely to be achieved on an operational basis and it is more likely that a core sample will explain about 70% of variation in whole tree pulp yield. Relationships which predict whole tree pulp yield from the cellulose content of cores cannot be applied to discs due to radial and longitudinal patterns of variation throughout the tree.

Whole tree extractives content can be predicted from cores but cores only explained 56% of variation in whole tree values. There was a significant inverse relationship between extractives content and pulp yield but the relationship was not sufficiently strong to be used as a predictive tool.

CHAPTER 3

3. Breeding for Pulp and Paper Properties [iv]

3.1 INTRODUCTION

Improving both the productivity and product quality of plantations is a goal of research, and tree improvement in particular. Historically, improving productivity has been the main priority of *E. nitens* breeding programs and this is reflected by the emphasis placed on growth in early genetic studies for this species (Pederick 1979; King and Wilcox 1988; Woolaston *et al.* 1991; Whiteman *et al.* 1992). The importance of quality was recognised through tree form in these studies, but it has not been until recently that wood properties have become an integral part of *E. nitens* breeding programs (Gea *et al.* 1997; Tibbits and Hodge 1998).

Wood properties are now widely recognised as important to end product value and overall profitability. Relationships between wood properties and profitability of kraft pulp production are well documented (Dean *et al.* 1990; Borralho *et al.* 1993; Greaves *et al.* 1997a), and all studies have found increased basic density and pulp yield to be important. For cold caustic soda, production relationships are less well defined but the important wood properties appear to be low density and long fibre length (Banham *et al.* 1995; Jones and Richardson 1999).

Relationships between wood properties and paper quality are more complex, sometimes antagonistic and less well defined (Raymond and Greaves 1997). Some paper properties appear to require thin walled fibres and low density wood while other paper properties require the opposite. For example, thin cell walls are required to produce paper with high strength because collapsed fibres have stronger bonding, whereas thicker cell walls are required to produce papers with high bulk (lower sheet density) and more porous properties (Arbuthnot 1991; Malan and Arbuthnot 1995; Cotterill and Macrae 1997; Kibblewhite *et al.* 1998). High bulk gives better printability and enhances softness in tissues (Dean 1995). The cross sectional dimensions of the fibre are therefore important determinants of paper quality.

[iv] Published: Kube, P. D., Raymond, C. A. and Banham, P. W. (2001). Genetic parameters for diameter, basic density, cellulose content and fibre properties for *Eucalyptus nitens*. Forest Genetics 8: 285-294.

This study calculates the genetic parameters of traits important for wood fibre production in *E. nitens*. The traits studied are those important for kraft pulp production (diameter, basic density, pulp yield), those important for cold caustic soda pulp production (basic density and fibre length), and those important for paper production (fibre length and fibre coarseness). Estimates are made of heritability, genetic and phenotypic correlations, and magnitude of genotype by environment interaction. Data for wood properties are based upon non-destructive sampling methods (Muneri and Raymond 2001; Raymond and Muneri 2001; Chapter 2 of this thesis). Cellulose content is used as an indicator of pulp yield. Measuring pulp yield directly is expensive and requires relatively large wood samples, and recent studies have shown cellulose content to be a reliable predictor of pulp yield in *E. nitens* (Wallis *et al.* 1996; Chapter 2 of this thesis).

3.2 MATERIALS AND METHODS

3.2.1 Trial establishment and assessment

The genetic material consisted of open pollinated progeny from 40 native forest families from the Toorongo Plateau in the central highlands of Victoria. Mother trees were growing as a pure stand in an open forest and stem diameters ranged from 35 to 110 cm. This location is described in Pederick (1979).

Progeny trials were established in 1984 on three sites in northern Tasmania, all with good soil fertility and good productivity (Table 3.1). Stocking at planting was 1100 trees ha^{-1} (3 m by 3 m spacing). The trial design was a randomised complete block with single tree plots and 16 replications per site. Survival at ages 6 and 12 years was 87% and 81% respectively.

Table 3.1. Location and description of trial sites.

	Dial	Gog	Kamona
Latitude (South)	41° 10'	41° 29'	41° 08'
Longitude (East)	146° 04'	146° 23'	147° 40'
Altitude (m)	100	300	160
Rainfall (mm per year)	1060	1200	1150
Mean maximum temp. warmest month (°C)	22.3	21.8	23.4
Mean minimum temp. coolest month (°C)	3.8	2.4	2.5
Site index (m) [i]	26.3	27.5	28.6
Parent material	mudstone	basalt	granite

[i] Site index is mean dominant height at age 15 years and was predicted using Farm Forestry Toolbox (Private Forests Tasmania 2001) after measuring the mean dominant height on each trial site.

All trees were measured for diameter at breast height (1.3 m) at 6 and 12 years. Wood properties measured were basic density, fibre length, fibre coarseness and cellulose content. Wood samples were taken at 12 years using two 12 mm

diameter bark to bark cores at a height of 0.9 m. One core was used to measure basic density, fibre length and fibre coarseness; and the second used to measure cellulose content. Core sampling at this height has been shown to be a reliable predictor of whole tree values of basic density (Raymond and Muneri 2001; Chapter 2 of this thesis), fibre length and fibre coarseness (Muneri and Raymond 2001) and cellulose content (Chapter 2). Trees less than 10 cm diameter were excluded from diameter and wood property assessments. Trees of this size were all strongly suppressed, had no diameter increment between ages 6 and 12, and had atypical wood properties. These trees were found to inflate error variances.

Basic density was defined as oven-dry wood mass per unit volume of green wood, and was measured using the water displacement method (Hendrichs and Larson 1970; TAPPI 1989). Between 5 and 13 trees per family per site were randomly sampled (average of 8). Following an initial analysis, 11 trees were excluded due to high residuals (greater than 3 standard deviations from mean). These trees had low diameters, very little diameter increment between 6 and 12 years, and very high density. The total number of trees and range of values in the final data set are shown in Table 3.2.

Fibre length and fibre coarseness were measured using a Kajaani FS200 fibre analyser (TAPPI 1991). When density measurements were completed, cores were macerated using a sodium hydroxide and peracetic acid digestion. Length-weighted average fibre lengths were used to place greater emphasis on uncut fibres. These measurements are produced routinely by the Kajaani FS200. Samples from Gog and Kamona were assayed on the same machine whilst those from Dial were assayed in a different laboratory. Five trees were randomly sampled per family per site. A total of 7 fibre coarseness records were discarded due to very high residuals (all had very high fibre coarseness). The total number of trees sampled and the range of values are shown in Table 3.2.

Table 3.2. Description of data used in analyses.

Trait		Min.	Mean	Max.	SD	N
D_6	Dbh age 6 (cm)	4.3	11.9	24.1	3.4	1159
D_{12}	Dbh age 12 (cm)	10.1	21.1	40.4	6.0	1160
D_{INC}	Dbh increment 6 to 12 (cm)	0.6	9.2	21.0	3.7	1158
BD	Basic density, core (kg m^{-3})	362	451	568	31	841
CEL	Cellulose, core (% kg kg^{-1})	38.0	41.5	45.4	1.4	545
FL	Fibre length, core (μm)	535	720	890	63.3	503
FC	Fibre coarseness, core (μg m^{-1})	34.0	55.5	77.5	6.84	497

Crude cellulose content (g cellulose per dry mass wood) was measured using the method of Wallis *et al.* (1997). Wood cores were dried at 27°C, fragmented in a disc pulveriser, and ground in a Wiley mill with a 1 mm mesh. Non-cellulosic compounds were solubilized by digestion in diglyme and hydrochloric acid and

the cellulose residue collected by filtration, washed and dried. Duplicate samples were assayed for 25% of samples as a general check on accuracy. An initial analysis was done (fitting the model 3.1 below) to identify outliers, on which a second set of duplicate samples were done. In total 45 samples were identified as outliers and repeated. Sample trees were the same as those used for fibre measurements (5 per family per site), with 42 additional samples included to obtain data on trees with outstanding growth.

3.2.2 Estimation of genetic parameters

Variances, covariances, correlations and errors for each site and each trait were estimated simultaneously by fitting multivariate multisite models. Multivariate analyses use information more efficiently and can improve the precision of genetic parameters when selected subsets of data are used (Dieters *et al.* 1999). An example of their use is shown and discussed in Apiolaza and Garrick (2001). Multivariate-multisite models allow all genetic correlations to be calculated directly, and use appropriate variance-covariance matrices for each site. These models treat measurements on different sites as different traits. Analyses were done using ASREML (Gilmour *et al.* 1999) and the model fitted was:

$$Y = \mu + SITE + REP + FAM(SITE) + \varepsilon \quad (3.1)$$

where Y is a vector of data for each trait; μ is the mean for each trait; SITE are site effects for each trait fitted as a fixed factor; REP are within site replicate effects for each trait fitted as a fixed factor; FAM(SITE) are within site family effects for each trait fitted as a random factor; and ε is a vector of residuals for each trait. Full inter-trait and inter-site variance and covariance matrices were fitted for the family and residual effects.

A second model was fitted to determine the importance of genotype by environment interactions and to estimate genetic correlations and heritabilities when data was pooled across sites. Error variances for each trait were all similar and therefore adjusting to a constant error variance was not considered necessary. The analysis was also done using ASREML and the model fitted was:

$$Y = \mu + SITE + REP + FAM + FAM.SITE + \varepsilon \quad (3.2)$$

where Y, μ, SITE, REP and ε are as previously defined; FAM are across site family effects for each trait fitted as a random factor; and FAM.SITE are site by family interaction effects for each trait fitted as a random factor. The model term FAM included an inter-trait variance and covariance matrix pooled across sites.

Heritabilities, site means and their standard errors were calculated using ASREML. Heritabilities for the individual site and multisite analyses were calculated as shown in models 3.3 and 3.4 respectively.

$$h^2 = \sigma^2_f / r\,(\sigma^2_f + \sigma^2_e) \quad (3.3)$$

$$h^2 = \sigma^2_f / r\,(\sigma^2_f + \sigma^2_{f.s} + \sigma^2_e) \quad (3.4)$$

Where h^2 is narrow sense heritability; σ^2_f, $\sigma^2_{f.s}$ and σ^2_e are, respectively, variance components for FAM, FAM.SITE and ε estimated in the models above; and r is the coefficient of relationship. The coefficient of relationship used was r = 0.4, and not r = 0.25 as is classically used for half-sib relationships (Falconer 1993). This assumes a selfing rate of approximately 30% (Griffin and Cotterill 1988) and is the approach that has been taken for many studies involving open pollinated eucalypts (e.g. Greaves *et al.* 1997b, Jordan *et al.* 1998, and Raymond and Schimleck 2001). For *E. globulus*, recent studies have suggested these assumptions about selfing rates are valid (Patterson *et al.* 2004). However, for *E. nitens* more recent studies have measured selfing rates of between 0 and 40% in a small clonal seed orchard (Grosser *et al.* 2001). This suggests the assumed selfing rate of 30% may be at the upper end of actual values, and therefore there is a risk that the heritabilities calculated in the current study may be slightly inflated.

3.2.3 Estimation of genetic gains

Genetic gains were estimated for diameter, basic density, cellulose and fibre length under different selection strategies. This was done by calculating individual tree breeding values for each trait and then using these breeding values to estimate gains in selected populations under different selection strategies.

Individual tree breeding values were calculated by fitting the following multivariate model using ASREML:

$$Y = \mu + SITE + REP + TREE + FAM.SITE + \varepsilon \quad (3.5)$$

where Y, μ, SITE, REP, FAM.SITE and ε are as previously defined and TREE are individual tree breeding values (additive genetic) for each trait. The terms TREE and ε included inter-trait variance and covariance matrices pooled across sites. Correlations were fixed to values calculated in model 3.2 and a coefficient of relationship of 0.4 was assumed for calculating additive genetic variances.

Five selection strategies were evaluated, with different sets of economic weights being applied for each strategy (see Table 3.7). The selection strategies were: (1) select for diameter only; (2) select for basic density only; (3) select for cellulose content only; (4) select for fibre length only; and (5) select using weights for diameter, density and cellulose to maximise profit from kraft pulp production. The weights used in strategy 5 are from Greaves *et al.* (1997a) and have been converted to standard deviation units.

Individual tree index values were calculated for each selection strategy as:

$$I = BV_D.W_D/\sigma_D + BV_{BD}.W_{BD}/\sigma_{BD} + BV_{FL}.W_{FL}/\sigma_{FL} + BV_{CEL}.W_{CEL}/\sigma_{CEL} \quad (3.6)$$

Where I is a unitless index value; BV is the breeding values for each trait (see Table 3.2 for definition of subscripts); σ is the additive genetic standard deviation

for each trait; and W is the economic weight defining the relative value of a standard deviation unit of each trait.

For each selection strategy, trees were sorted by index value (*I*) and the average breeding values of the top 60 trees was calculated. This represents a selection intensity of 5% and simulated selecting 20 trees for a clonal seed orchard with a restriction that no family be represented by more than two individuals. The average value of the top 60 trees was expressed as a percentage gain over the unselected population

Wood consumption (WC) is a variable used to measure the quality of wood for kraft pulping (Borralho *et al.* 1993; Macrae *et al.* 1999) and was calculated for each of the five selection strategies. WC defines the volume of wood required to make one oven dry tonne of kraft pulp (in units of m^3 per tonne pulp) and was calculated using the definition of Borralho *et al.* (1993) which is:

$$WC = 1000 / (DEN \,.\, PY) \quad (3.7)$$

Where DEN and PY are, respectively, wood density and pulp yield at harvest age. DEN and PY were estimated from the selection traits BD and CEL. When calculating WC for each selection strategy, it was assumed genetic correlations between selection and harvest age traits were $r_g = 0.8$ and base levels for DEN and PY were 480 kg m^{-3} and 53% (Table 2.2).

3.3 RESULTS

3.3.1 Site differences

There were statistically significant differences between sites for all traits (Table 3.3). Growth rates at a typical pulpwood harvest age (15 years) were predicted to be 21, 23 and 25 m^3 ha^{-1} $year^{-1}$ for Dial, Gog and Kamona respectively.[v] Basic density, cellulose content and fibre coarseness were highest at Gog, where density was nearly 3% higher, cellulose content 7% higher and fibre coarseness 9% higher than the average of the other sites. Differences in pulp yield between the best and poorest sites are predicted to be 2.2% using relationships defined in Chapter 2. Fibre length was significantly shorter at Dial Range (difference of 14%). However, the assays for this site were done in a different laboratory and therefore these differences may not be true site differences.

[v] Volumes were predicted using Farm Forestry Toolbox (Private Forests Tasmania 2001) from mean dominant height data and basal area data.

Table 3.3. Trait means for each site.

Trait	Dial	Gog	Kamona	SED [1]
D_6 (cm)	10.3	10.2	14.8	1.6
D_{12} (cm)	20.3	22.8	25.2	3.1
D_{INC} (cm)	10.0	12.6	10.3	1.9
BD (kg m^{-3})	447	477	457	15
CEL (% kg kg^{-1})	40.3	43.0	41.3	0.7
FL (μm)	653	767	763	34
FC (μg m^{-1})	51.0	58.1	55.0	4.0

[1] Standard error of difference, probability of a larger value = 0.05.

3.3.2 Heritability

Individual site heritabilities for diameter at 6 years (Table 3.4) were low to moderate (0.12 to 0.29), but had increased substantially by 12 years (0.32 to 0.45). At 12 years, differences in heritability between sites were less than those at 6 years. In a combined site analysis, heritabilities for diameter at 6 and 12 years were 0.17 and 0.39 respectively (Table 3.4).

Individual site heritabilities for basic density were high to very high, ranging from 0.50 to 0.96 (Table 3.4). Estimates varied significantly across sites, with Gog having higher heritability than other sites. This difference was primarily due to differences in additive genetic variances across sites. In a combined site analysis the heritability for basic density was 0.51 (Table 3.4) which was less than the average for individual sites (0.70). Genotype by environment interaction was present for this trait (see section 3.3.4) and the different heritabilities presumably represent a shift of additive genetic variance to family by site variance.

Cellulose content also had high to very high individual site heritabilities, ranging from 0.52 to 1.00 (Table 3.4). As with basic density, estimates across different sites varied significantly, with one site (Dial) having a significantly lower heritability. This was primarily caused by a lower additive genetic variance at that site. Differences in error variance between sites may have been caused by differences in laboratory techniques. The Kamona site was the final site to be done and laboratory equipment and operator skills were improved. As for basic density, the heritability for cellulose content in a combined site analysis was less than the average for individual sites (0.56 compared to 0.79, Table 3.4) which is presumably caused by genotype by environment interaction.

Table 3.4. Variance components and heritabilities (± standard errors) for stem diameter (D), basic density (BD), cellulose content (CEL), fibre length (FL) and fibre coarseness (FC).

Trait	Site	σ^2 family	σ^2 family.site	σ^2 error	h^2
D_6 (cm)	Dial	0.31 ± 0.20		6.23 ± 0.46	0.12 ± 0.08
	Gog	0.82 ± 0.34		6.24 ± 0.48	0.29 ± 0.10
	Kamona	0.81 ± 0.46		11.25 ± 0.91	0.17 ± 0.09
	All sites	0.58 ± 0.21	0.05 ± 0.13	7.84 ± 0.35	0.17 ± 0.06
D_{12} (cm)	Dial	4.35 ± 1.54		25.0 ± 1.8	0.37 ± 0.12
	Gog	6.09 ± 2.09		28.0 ± 2.1	0.45 ± 0.13
	Kamona	5.64 ± 2.78		38.6 ± 3.1	0.32 ± 0.12
	All sites	5.56 ± 1.57	0.00	29.9 ± 1.3	0.39 ± 0.10
D_{INC} (cm)	Dial	2.76 ± 0.86		10.39 ± 0.76	0.53 ± 0.14
	Gog	2.49 ± 0.82		10.38 ± 0.83	0.48 ± 0.15
	Kamona	2.02 ± 0.78		10.39 ± 0.76	0.35 ± 0.13
	All sites	2.61 ± 0.71	0.00	10.95 ± 0.48	0.48 ± 0.11
BD (kg m^{-3})	Dial	177 ± 62		716 ± 63	0.50 ± 0.16
	Gog	374 ± 110		602 ± 55	0.96 ± 0.18
	Kamona	199 ± 71		587 ± 59	0.63 ± 0.17
	All sites	188 ± 58	59 ± 26	673 ± 39	0.51 ± 0.13
CEL (% kg kg^{-1})	Dial	0.26 ± 0.12		1.00 ± 0.13	0.52 ± 0.21
	Gog	0.55 ± 0.18		1.05 ± 0.12	0.86 ± 0.20
	Kamona	0.58 ± 0.18		0.81 ± 0.09	1.05 ± 0.21
	All sites	0.37 ± 0.12	0.07 ± 0.06	1.22 ± 0.09	0.56 ± 0.15
FL (μm)	Dial	251 ± 190		2276 ± 297	0.25 ± 0.19
	Gog	667 ± 233		1409 ± 169	0.80 ± 0.21
	Kamona	607 ± 231		1631 ± 194	0.68 ± 0.21
	All sites	502 ± 166	0.00	2199 ± 161	0.46 ± 0.13
FC (μg m^{-1})	Dial	0.0 ±		28.32 ± 3.32	0.0 ±
	Gog	6.46 ± 2.80		21.49 ± 2.71	0.58 ± 0.23
	Kamona	4.38 ± 2.34		23.90 ± 2.99	0.39 ± 0.13
	All sites	0.95 ± 0.99	0.98 ± 1.43	32.14 ± 0.32	0.07 ± 0.07

Fibre length had moderate to very high individual site heritabilities, with estimates ranging from 0.25 to 0.80 (Table 3.4). The low heritability at the Dial site was due to a much lower additive genetic variance and a higher error variance. Fibre lengths for this site were measured in a different laboratory and this may have contributed to these differences. In a combined site analysis the heritability for fibre length was slightly lower than the average of individual sites (0.46 compared with 0.58, Table 3.4) but these differences are not statistically different.

Fibre coarseness had variable heritabilities with values being moderately high at two sites, but zero at the third site (Table 3.4). In a combined site analysis the heritability was low (0.07) and not significantly different from zero (Table 3.4). Fibre coarseness has been found to be an unreliable trait because it does not distinguish between small fibres with thick walls and large fibres with thin walls (Arbuthnot 1991; Muneri and Raymond 2001). In this study, genetic correlations

for fibre coarseness between sites were zero (Table 3.6) indicating that a different trait is being measured at each site. Therefore, although there appears to be some genetic control over the cross sectional dimensions of fibres, the response is highly dependent on the site conditions.

3.3.3 Correlations

There were adverse genetic correlations between diameter-density. Correlations were variable across sites but mostly strong. For diameter at 12 years and density, values for individual sites ranged from –0.16 to –0.77, and in a pooled analysis the correlation was –0.57 (Table 3.5). Correlations tended to be more negative at a younger age (–0.72 compared with –0.57 in the combined site analysis). Correlations were also examined when using density after the removal of extractives (see section 5.2.2 for methods) to see if extractives content influenced this correlation. However, relationships were identical for both unextracted and extracted wood density and therefore the adverse relationship between diameter and density appears to be uninfluenced by extractives content.

Table 3.5. Genetic correlations (r_G) with standard errors above diagonal and phenotypic correlations (r) below diagonal.

Site		D_6	D_{12}	BD	CEL	FL	FC
Dial	D_6		0.79 ± 0.14	-0.54 ± 0.29	0.73 ± 0.32	-0.20 ± 0.43	0 ± 0
	D_{12}	0.79 *		-0.16 ± 0.24	0.86 ± 0.16	0.36 ± 0.34	0 ± 0
	BD	-0.21 *	-0.17 *		-0.26 ± 0.27	0.75 ± 0.32	0 ± 0
	CEL	0.09	0.23 *	0.09		-0.13 ± 0.26	0 ± 0
	FL	-0.14 *	0.08	0.23 *	0.48 *		0 ± 0
	FC	0.19 *	0.07	0.01	-0.21 *	-0.12	
Gog	D_6		0.98 ± 0.03	-0.66 ± 0.18	0.83 ± 0.14	0.49 ± 0.23	0.18 ± 0.30
	D_{12}	0.87 *		-0.77 ± 0.13	0.81 ± 0.12	0.51 ± 0.20	0.12 ± 0.27
	BD	-0.13	-0.12		-0.53 ± 0.18	-0.17 ± 0.22	0.11 ± 0.25
	CEL	0.18	0.35 *	0.06		0.86 ± 0.16	0.22 ± 0.25
	FL	0.11	0.26 *	0.14	0.45 *		0.47 ± 0.24
	FC	0.03	0.06	0.16	0.11	0.22 *	
Kamona	D_6		1.00 ± 0.04	-0.94 ± 0.24	0.64 ± 0.24	0.29 ± 0.32	-0.77 ± 0.41
	D_{12}	0.89 *		-0.71 ± 0.20	0.62 ± 0.18	0.27 ± 0.26	-0.45 ± 0.33
	BD	-0.02	-0.03		-0.19 ± 0.23	-0.01 ± 0.21	0.33 ± 0.29
	CEL	0.25 *	0.40 *	0.09		0.41 ± 0.20	-0.19 ± 0.27
	FL	0.26 *	0.38 *	0.22 *	0.49 *		-0.68 ± 0.28
	FC	0.17 *	0.21 *	0.26 *	0.00	0.04	
All sites	D_6		0.97 ± 0.02	-0.72 ± 0.14	0.82 ± 0.11	0.34 ± 0.21	-0.20 ± 0.35
	D_{12}	0.82 *		-0.57 ± 0.15	0.79 ± 0.10	0.37 ± 0.19	-0.11 ± 0.32
	BD	-0.14 *	-0.11		-0.45 ± 0.18	0.15 ± 0.22	0.29 ± 0.32
	CEL	0.14 *	0.32 *	0.11		0.54 ± 0.16	-0.07 ± 0.33
	FL	0.02	0.14 *	0.26 *	0.46 *		0.39 ± 0.33
	FC	0.00	0.06	0.22 *	0.05	0.25 *	

* Significantly different from zero at P<0.05.

Genetic correlations between density and cellulose were also adverse and variable across sites (Table 3.5). Values ranged from –0.19 to –0.53 and in a pooled analysis the correlation was –0.45.

There were favourable genetic correlations between diameter and cellulose, diameter and fibre length, and between fibre length and cellulose (Table 3.5). For diameter and cellulose, values for individual sites were significantly different, but all were strongly positive. Values ranged between 0.62 and 0.86, and in a pooled analysis the correlation was 0.79. Correlations between fibre length and diameter were variable across sites (–0.20 to 0.49) but in a pooled analysis this correlation was 0.37. Similarly, correlations between fibre length and cellulose were highly variable across sites (–0.13 to 0.86) and strongly favourable in the pooled analysis (0.54).

Genetic correlations between fibre length and density were highly variable across sites, ranging from –0.17 to 0.75, and in a pooled analysis the correlation was not significantly different from zero (Table 3.5). Genetic correlations between fibre coarseness and other wood traits formed no pattern with correlations often being completely opposite on different sites.

Phenotypic correlations between diameter at 6 and 12 years were strong, but other relationships were weak (Table 3.5). The strongest were those between fibre length and cellulose content ($r = 0.45$ to 0.49), and diameter at 12 years and cellulose content ($r = 0.23$ to 0.40). There were significant negative correlations between diameter and basic density at two sites, although the relationship was very weak. Phenotypic correlations of fibre coarseness with other traits were not consistent across sites. A positive relationship between fibre coarseness and density could be expected since high density wood usually has thicker cell walls (Malan *et al.* 1994), however, this relationship was always weak and significant on two sites only.

3.3.4 Genotype by environment interaction

There were no significant genotype by environment interactions for diameter at 6 years and diameter at 12 years. Family by site variance was either zero or extremely low (Table 3.4) and genetic correlations between sites were very high (Table 3.6). Similarly, fibre length had no genotype by environment interaction and a very high genetic correlation between sites (Tables 3.4 and 3.6).

Genotype by environment interaction for basic density was relatively small but significant. Family by site variance consisted of 6% of total variation (Table 3.4), and genetic correlations between sites ranged between 0.67 and 0.92 (Table 3.6). The interaction appeared to be caused by minor rank changes from many families. Excluding groups of families did not substantially reduce the interaction. At best, dropping the most interactive family reduced the family by site variance to 5% of

total, but dropping other families made very little difference. Scale effects can also cause genotype by environment interaction, where genetic expression on one site may be much stronger than other sites. However, for these data scale effects contributed very little to the interaction. After weighting the data by the site standard deviation, family by site variance reduced by only 0.5%.

Table 3.6. Genetic correlations (± standard error) between sites.

Trait	Dial & Gog	Dial & Kamona	Gog & Kamona
D_6	1.08 ± 0.31	0.59 ± 0.43	1.16 ± 0.25
D_{12}	1.09 ± 0.10	0.93 ± 0.13	1.14 ± 0.12
D_{INC}	1.09 ± 0.07	0.98 ± 0.11	1.13 ± 0.11
BD	0.73 ± 0.15	0.67 ± 0.19	0.92 ± 0.11
CEL	0.77 ± 0.23	0.91 ± 0.19	0.89 ± 0.15
FL	1.22 ± 0.37	1.19 ± 0.40	1.36 ± 0.29
FC	0 ±	0 ±	-0.22 ± 0.32

Genotype by environment interaction for cellulose content was also relatively small but significant. Family by site variance consisted of 4% of total variation (Table 3.4), and genetic correlations between sites ranged from 0.77 to 0.91 (Table 3.6). This interaction appears to be mainly caused by scaling effects. After weighting the data by the site standard deviation family by site variance reduced to less than 2% of total.

3.4 DISCUSSION

3.4.1 Comparing genetic parameters

Published heritability estimates for *E. nitens* diameter cover a wide range (0.11 to 0.55) and those from this study fall within that range. Six year diameters are at the bottom end of the range and are comparable to those of Woolaston *et al.* (1991), Whiteman *et al.* (1992), Johnson (1996) and Gea *et al.* (1997). Twelve year diameters are at the upper end of the range and are comparable to some of the basal area estimates of Tibbits and Hodge (1998). The published information generally confirms the trend of increasing heritability with age.

Reported heritabilities for *E. nitens* basic density also cover a wide range (0.17 to 0.83) and those from this study fall in the mid to upper end of that range (Greaves *et al.* 1996; Gea *et al.* 1997; Tibbits and Hodge 1998). As in this study, some very high individual site heritabilities have been reported but estimates tend to be lower in a combined site analysis. In the most comprehensive study for *E. nitens* basic density (Tibbits and Hodge 1998) the combined site heritability (0.43 ± 0.09) was very similar to that for this current study (0.51 ± 0.13). The very high heritability estimate from the Gog site is not without precedent; similar values are reported for *E. globulus* (Muneri and Raymond 2000).

Heritabilities for cellulose content from this study are higher than other published estimates of both cellulose content and pulp yield for eucalypts. For pulp yield, most estimates are in the range of 0.30 to 0.63, although some heritabilities as low as 0.02 have been reported (Clarke 1990; Dean *et al.* 1990; Borralho *et al.* 1993; Tibbits and Hodge 1998; Raymond *et al.* 2001). Published heritabilities for cellulose content (all for *E. globulus*) cover a similar range, varying from 0.31 to 0.57 (Cotterill and Brolin 1997; Raymond and Schimleck 2001). The combined site heritability for cellulose content in this study is higher than the pulp yield estimate for *E. nitens* of Tibbits and Hodge (1998), but differences are not large (0.56 ± 0.15 compared with 0.38 ± 0.08). The relatively high heritability in this current study may be a result of the methodology used. Most other studies have not used as many samples and none have used the Wallis *et al.* methodology, which is less influenced by hemicellulose residues (Wallis *et al.* 1997).

Heritabilities for fibre length from this study (which ranged from 0.25 to 0.80) tend to be higher than other reported values for eucalypts. Published estimates are all for single sites and vary between 0.30 and 0.54 (Dean *et al.* 1990; Cotterill and Brolin 1997; Raymond *et al.* 1998), with the only estimate for *E. nitens* being 0.32 (Dean *et al.* 1990). For fibre coarseness of eucalypts, published heritabilities vary between 0.03 and 0.40 (Cotterill and Brolin 1997; Dean *et al.* 1990; Raymond *et al.* 1998), with the only estimate for *E. nitens* being 0.03 (Dean *et al.* 1990). However, all are based on single sites and probably do not reflect exploitable genetic variation given the poor across site repeatability found in this study.

Published estimates of genetic correlations for eucalypts are highly variable. Those between diameter and density are usually negative but range between 0 and –0.6 (Clarke 1990; Dean *et al.* 1990; Gea *et al.* 1997; Tibbits and Hodge 1998; Muneri and Raymond 2000). Individual site estimates from this study were also variable (–0.16 to –0.77) but generally more strongly negative. For diameter and pulp yield of *E. nitens*, published genetic correlations are positive (Tibbits and Hodge 1998). Those from this study were also positive but were much stronger (0.79 ± 0.10 compared with 0.24 ± 0.12), although this may be partly due to inherently stronger relationships when measuring cellulose content as compared with pulp yield. For other eucalypts estimates are negative and range from –0.16 to –0.54 (Clarke 1990; Dean *et al.* 1990; Raymond *et al.* 2001). For basic density and pulp yield, published genetic correlations for eucalypts are either zero or positive and range between 0 and 0.7 (Dean *et al.* 1990; Tibbits and Hodge 1998; Raymond *et al.* 2001). This study is unique in finding strongly negative correlations between these traits.

There are a number of possible reasons for variability in estimates of genetic correlations. It may be due to inherent variation between species and populations. Published data suggests species differences may exist (e.g. differences between

E. nitens and *E. globulus*), but no studies have examined differences between races within a species. It may also be due to variation in the degree of genetic expression across sites. Sites on which genetic expression is high would also be expected on have higher genetic correlations. Another reason contributing to variable genetic correlations could be the quality and size of data sets. Some estimates of genetic correlations are made using small or truncated data sets because wood testing is relatively costly and this may bias some estimates. Regardless of the reasons for variable genetic correlations, it appears unwise for tree breeders to assume standard correlations when making selections. A safer approach would be to assess a sample of the population to estimate true genetic correlations and apply these to the estimation of breeding values.

Table 3.7. Genetic gains (% of mean value) using different selection strategies.

Index	Relative weights [i]	D_{12}	BD	CEL	FL	Wood consumption [iii] (m3 per t)
1. Diameter only	1: 0: 0: 0	20	-4	3	2	3.8 (+1%)
2. Basic density only	0: 1: 0: 0	-15	8	-2	1	3.6 (–3%)
3. Cellulose content only	0: 0: 1: 0	17	-3	3	3	3.7 (–1%)
4. Fibre length only	0: 0: 0: 1	10	1	2	6	3.7 (–2%)
5. Kraft pulp production [ii]	3: 3: 1: 0	13	1	2	4	3.6 (–3%)

[i] Relative importance of a one standard deviation gain for D_{12}, BD, CEL and FL respectively.

[ii] Economic weights to maximise profit per ha for unbleached kraft pulp production. Values were taken from Greaves *et al.* (1997a) and converted to standard deviation units.

[iii] Wood consumption measures the volume of wood required to produce one tonne of kraft pulp.

3.4.2 Gains from selection

Large simultaneous gains cannot be obtained in all traits due to negative correlations between basic density and diameter, and basic density and cellulose content (Table 3.7). Gains in diameter of 20% are possible, although selection for diameter alone will cause a 4% decline in basic density and a decrease in kraft pulping wood quality. Similarly, basic density gains of 8% are possible if selecting for this trait alone, but this will result in a fall in diameter and cellulose content of 15% and 2% respectively. Favourable correlations between diameter and cellulose content result in improved cellulose content for any index with a growth emphasis. Fibre length will increase under all selection strategies due to favourable correlations with diameter and generally favourable correlations with both density and cellulose content. Gains in the wood quality for pulping (as measured by wood consumption) are best when using the basic density and kraft pulp indices (Table 3.7), although the associated decline in growth rate when selecting for density alone is unlikely to be advantageous to a forest grower.

Understanding the economic value of each trait is essential for multitrait selection because adverse genetic correlations require trade-offs between traits. This can be demonstrated using the Kraft pulp economic weights of Greaves *et al.* (1997a). Using these weights, it can be shown that the economic gain (expressed as profit per ha) when selecting for diameter, basic density or cellulose content alone (indices 1 to 3 in Table 3.7) is only half of that when selecting on the Kraft pulp index (index 5 on Table 3.7). When using this index the gains for diameter, basic density and cellulose content were 13%, 1% and 2% respectively (Table 3.7). Under this index the largest trade-off in potential gain was in basic density.

3.4.3 Implications for breeding programs

The strong adverse genetic correlation between basic density and diameter is of greatest importance to breeding programs. Selection for diameter alone will result in a decline in basic density and this will compromise the profitability of tree breeding for most enterprises. Therefore it is important that tree breeding programs do two things. Firstly, there must be a sound assessment of the economic importance of basic density, and appropriate economic weights applied. In the preceding section, the economic weights of Greaves *et al.* (1997a) have been used but different weights are appropriate for different enterprises (see Borralho *et al.* 1993). Secondly, there should be routine screening for basic density to find good combinations of diameter and basic density (i.e. to find correlation breakers). For example, under a different set of economic weights it can be shown that gains of 5% can be obtained in both diameter and basic density.

Cellulose content has been shown to be a reliable indicator of kraft pulp yield (Wallis *et al.* 1996; Chapter 2 of this thesis) and is highly heritable. On two sites almost all variation was explained by additive genetic variance. It is also highly correlated with other traits. This study found favourable genetic correlations between growth and cellulose content and this is supported by other studies in *E. nitens* (Tibbits and Hodge 1998). However, contrary to other studies, correlations between cellulose content (or pulp yield) and wood density were found to be weakly negative. Breeding programs that do not select directly for cellulose content will probably make reasonable gains in this trait. Strong favourable correlations between diameter and cellulose content will lead to a correlated response for cellulose irrespective of the weaker adverse correlation with basic density. Data from this study showed that selecting for diameter and basic density alone will deliver 85% of gains in cellulose content. A similar result is reported by Greaves *et al.* (1997a), where selecting on an index that included diameter and basic density delivered 95% of economic gains to a kraft pulp producer.

Fibre length is also highly heritable, but the nature of genetic correlations is ambiguous in this study. It appears the genetic expression of this trait is sensitive

to site, as indicated by different heritabilities and different patterns of genetic correlations across sites. Despite this, it appears that breeding programs can assume fibre length will increase under all selection regimes without directly selecting for this trait (see Table 3.7).

Fibre coarseness was an unreliable trait in this study. The measure used here (Kajaani fibre coarseness) appeared to be a different trait on different sites. Problems with Kajaani fibre coarseness have been noted in other studies (Arbuthnot 1991), and are caused by the confounding of small diameter/thick walled fibres and large diameter/thin walled fibres. Fibre coarseness is an important trait for paper properties (Arbuthnot 1991; Kibblewhite *et al.* 1998) and data from this study suggests genetic variation is present. Therefore another low cost, non-destructive and rapid measurement technique is required if this trait is to be exploited in breeding programs.

Paper quality is strongly influenced by fibre properties (e.g. Cotterill and Macrae 1997; Kibblewhite *et al.* 1998). Higher wood density is known to increase the profitability of pulp production, but there is a risk that higher density may adversely affect some fibre qualities. For example, high density wood may have thick fibres resulting in either paper of lower strength or in increased production costs to manufacture paper to given strength standards (Cotterill and Macrae 1997). Therefore there is a need to extend work on breeding objectives from the production of pulp (e.g. Greaves *et al.* 1997a) to the production of paper.

3.5 CONCLUSION

Diameter growth is under moderate genetic control with genetic expression increasing with age. Basic density, cellulose content and fibre length are under strong genetic control. Breeding programs of *E. nitens* have the potential to make gains in these traits. Fibre coarseness measured on the Kajaani fibre analyser is an unreliable trait, presumably due to confounding of small diameter/thick walled fibres and large diameter/thin walled fibres. Favourable genetic correlations were found between diameter and cellulose, diameter and fibre length and between cellulose and fibre length; adverse correlations between diameter and density, and between density and cellulose; and variable correlations between fibre length and density. There is evidence that genetic correlations between traits are variable and standard correlations cannot be assumed. Therefore tree breeders should assess wood properties if for no other reason than to estimate genetic correlations for their population and determine the potential for declining wood quality due to adverse genetic correlations.

CHAPTER 4

4. Breeding to Minimise the Effects of Collapse [vi]

4.1 INTRODUCTION

Eucalyptus nitens has many of the characteristics required for high quality appearance products. However, in saw milling trials the major causes of downgrade were knots and checking (McKimm *et al.* 1988, Waugh and Yang 1994, McKenzie *et al.* 2002a). Knots are a problem in *E. nitens* because this species retains dead branches, but this can be being managed silviculturally by using pruning regimes (Neilsen and Pinkard 2000).

Checking is a problem that occurs during drying and refers to the separation of the fibres along the grain to form a crack in the timber. These cracks can occur both internally and on the surface but do not extend through the piece of timber (Hillis and Brown 1978, Jacobs 1979). Collapse, which is a type of shrinkage in wood caused by the buckling of the cell walls and flattening of the lumens, is recognised as a major cause of checking (Campbell and Hartley 1978, Jacobs 1979, Chafe *et al.* 1992, Ilic 1999). Collapse is different from normal shrinkage in that it occurs as moisture is removed from the cell lumens (i.e. above fibre saturation point). Normal shrinkage occurs after water has been removed from the lumens, and is caused by the removal of water from the cell wall. Collapse is caused by hydrostatic tension forces within the cell and, when capillary size is small and cell walls thin, these forces exceed the compressive strength of the cell wall leading to a flattening of the cell (Chafe 1985, Chafe *et al.* 1992). Collapse in *E. regnans* has been found to be related to basic density, moisture content and shrinkage. However, these properties do not appear to explain any more than 20% of variation in collapse (Chafe 1985, Ilic 1999).

Collapse has been found to vary within trees. Problems appear to be most severe near the stump, and decrease along the length of the stem (Pankevicius 1961, Chafe 1985, Purnell 1988, Raymond and Savage, unpublished data.). This may be a result of decreasing moisture content (lower lumen saturation) and higher

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wood density (thicker cell walls) along the length of the stem (Chafe 1985). Regardless of the cause, this variation has serious implications for eucalypt sawlog plantations because the pruning regimes used for these plantations concentrate investment on the bottom log (Neilsen and Pinkard 2000), which is the part of the tree where the problem will be at its worst.

Checking and collapse have been recognised as problems since utilisation of eucalypts began. Treatments to address these problems were first developed in 1917 and have been the subject of ongoing research (Chafe *et al.* 1992). Essentially two methods for managing these problems have been developed. The first of these is the use of appropriate sawing techniques. Collapse manifests differently on radial (quarter sawn) and tangential (back sawn) faces of sawn wood (Campbell and Hartley 1978, Jacobs 1979, Chafe *et al.* 1992). On the quarter sawn face, collapse appears as a corrugated or 'washboard' surface with little or no surface checking. This problem can be easily overcome by cutting over size and then planing, although it does cause lower recovery. On the back sawn face collapse can cause internal and surface checking which is sometimes very severe. This can be partially managed by cutting thinner boards (25 mm) and by carefully air-seasoning prior to kiln-drying. The second method used to manage checking and collapse is 'reconditioning' which involves steaming boards for 2 to 6 hours at atmospheric pressure (Jacobs 1979, Chafe *et al.* 1992). Steaming in this way softens cell walls without saturating the cell lumens and allows buckled cell walls to resume their normal shape. Reconditioning can close checks but the fractures remain and for some applications, such as moulding, this does not solve the problem.

Although sawing techniques and reconditioning have allowed the commercial utilisation of what were once uncommercial species (Jacobs 1979), they do not solve all problems and other management techniques are needed (Chafe *et al.* 1992). This is likely to be also true for plantation grown *E. nitens* wood. Log sizes may be too small to quarter saw (Waugh and Yang 1994) and therefore the saw miller will have fewer management options (Jacobs 1979). Furthermore, although saw milling studies on *E. nitens* have indicated checking will be within manageable limits (Waugh and Yang 1994, McKenzie *et al.* 2002a), other studies suggest there will be severe checking problems on some sites which will limit its use as appearance grade timber (Shelbourne *et al.* 2002).

Tree breeding has been suggested as a potential method for managing checking and collapse. Many studies report large variation between trees (e.g. Purnell 1988, Chafe *et al.* 1992) and genetic variation is usually suggested as the cause. Nevertheless, studies on genetic variation in checking and collapse appear limited and tree breeding is not being used to manage collapse. Published genetic studies in eucalypts appear limited to a provenance study for *E. delegatensis* (King *et al.*

1993), and a small study (5 seedlots) for *E. nitens* (Purnell 1988). No studies appear to have been done on the genetic parameters of checking or collapse.

This study evaluates tree breeding as a tool to manage collapse and checking in *E. nitens*. There were three aims to this study. The first was to calculate the degree of genetic control and the amount of genotype by environment interaction for collapse. The second was to determine relationships between collapse and traits that are used in existing breeding programs (that is growth, basic density and pulp yield content). And the third aim was to assess the potential of tree breeding to change the incidence of collapse (and therefore checking), and to explore options for using collapse in a breeding program.

4.2 MATERIAL AND METHODS

4.2.1 Trial establishment and assessment

The genetic material was open-pollinated progeny of 40 native forest families from the Toorongo Plateau in the central highlands of Victoria and the location is described in Pederick (1979). Mother trees were growing as a pure stand in an open forest and stem diameters ranged from 35 to 110 cm.

Progeny trials were established in 1984 on three sites in northern Tasmania, all with good good productivity (Table 4.1). Stocking at planting was 1111 trees ha^{-1} (3 m by 3 m spacing) and survival at age 12 years was 81%. The trial design was a randomised complete block with single tree plots and 16 replications per site. Fifteen of the 40 families were only planted at two sites. The missing families were spread, in different combinations, across all sites and so every site had at least 35 families. Traits measured were diameter at breast height, basic density, cellulose content and collapse, and these are summarised in Table 4.2.

Table 4.1. Location and description of trial sites.

	Dial	Gog	Kamona
Latitude (South)	41° 10'	41° 29'	41° 08'
Longitude (East)	146° 04'	146° 23'	147° 40'
Altitude (m)	100	300	160
Rainfall (mm per year)	1060	1200	1150
Mean maximum temp. warmest month (°C)	22.3	21.8	23.4
Mean minimum temp. coolest month (°C)	3.8	2.4	2.5
Site index (m) [i]	26.3	27.5	28.6
Parent material	mudstone	basalt	granite

[i] Site index is mean dominant height at age 15 years and was predicted using Farm Forestry Toolbox (Private Forests Tasmania 2001) after measuring the mean dominant height on each trial site.

All trees were measured for diameter at breast height (1.3 m) at 12 years. Trees less than 10 cm diameter were excluded from diameter and wood property

assessments. Trees of this size were all strongly suppressed with no diameter increment between ages 6 and 12, and had atypical wood properties. These trees were found to inflate error variances.

Table 4.2. Description of data (SD = standard deviation, n = number of samples).

Trait		Min.	Mean	Max.	SD	N
D	Dbh age 12 (cm)	10.1	21.1	40.4	6.0	1160
BD	Basic density (kg m^{-3})	362	451	568	31	841
CEL	Cellulose content (% kg kg^{-1})	38.0	41.5	45.4	1.4	545
COL	Tangential collapse (%)	0	16.2	37.5	7.6	806

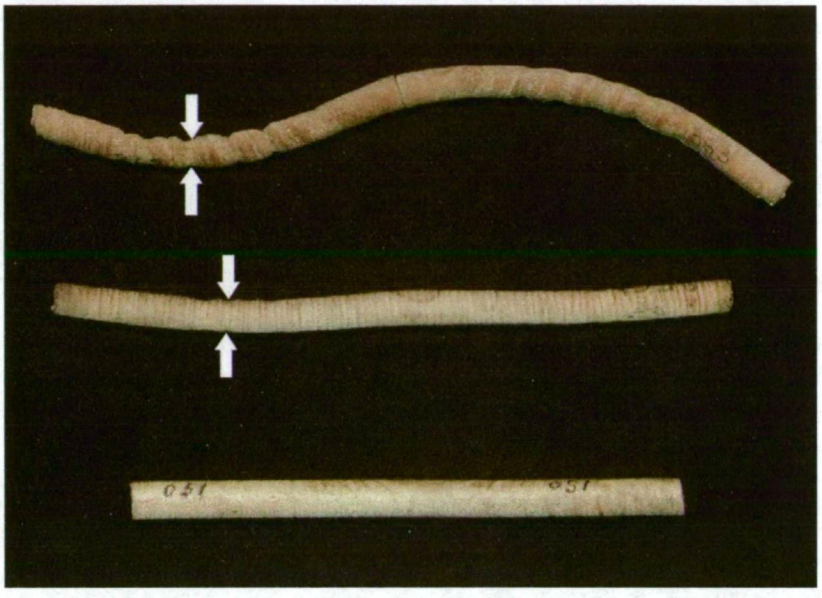
Basic density was measured at 12 years using a 12 mm diameter bark to bark core taken at a height of 0.9 m. Core sampling at this height has been shown to be a reliable predictor of whole tree values of basic density (Raymond and Muneri 2001, Chapter 2 of this thesis). Basic density was defined as oven-dry wood mass per unit volume of green wood, and was measured using the water displacement method (Hendrichs and Larson 1970; TAPPI 1989). Samples were taken from all sites and between 5 and 13 trees per family per site were randomly sampled (average of 8). Following an initial analysis, 11 trees were excluded due to high residuals (greater than 3 standard deviations from mean density). These trees had low diameters, very little diameter increment between 6 and 12 years, and very high density.

Crude cellulose content (g cellulose per wood dry mass) was assessed at 13 years using a 12 mm bark to bark core taken at a height of 0.9 m. Cores taken at this height are known to be reliable predictors of whole tree cellulose content (Chapter 2 of this thesis). Cores were dried at 27°C, ground and assayed using the method of Wallis *et al.* (1997). Five trees were randomly sampled per family from each site. More details of the sampling and analysis are given in section 3.2.1.

Tangential collapse was assessed on the same core as that used to measure basic density. Core sampling at this height has been shown to reliably predict average collapse in the bottom 6 m of the stem for *E. nitens* (Raymond and Savage, unpublished data). After drying green cores at 105°C, bands of very high shrinkage were observed on the cores (Figure 4.1). These shrinkage bands recovered fully after steam reconditioning for one hour and therefore it was assumed that the observed bands were due to collapse and not collapse-free or normal shrinkage or tension wood (Chafe 1985, Chafe *et al.* 1992). The degree of collapse was quantified by measuring tangential diameter at the narrowest point of each section of the bark to pith core (i.e. two measurements per tree). This diameter was then expressed as the percentage loss relative to the tangential diameter at the pith after drying. The tangential diameter of the pith did not

change before and after reconditioning. Sample trees were the same as those used for basic density measurements (an average of 8 trees per family per site).

Figure 4.1. Location of shrinkage bands (see arrows) measured to assess collapse. The upper core is a sample with very high shrinkage bands and very high distortion after drying. The middle core is a sample with very low shrinkage bands and low distortion. The lower core is a sample following steam reconditioning where shrinkage bands and distortion have recovered.



Wood densities measured using x-rays techniques on SilviScan-2 (Evans *et al.*, 2000) were used for a small part of this study. Assessing wood density using x-rays allows very specific measurements to be made on individual growth rings and on variation within growth rings. Relationships between these measurements and collapse were explored. Wood samples were from an additional bark to bark core taken at a height of 0.9 m. This core was dehydrated in ethanol and dried at 25°C. A thin bark to pith strip was cut from this core (2 mm tangentially and 7 mm longitudinally) and density was then measured at 0.05 mm intervals using Silviscan-2. For this study density measurements were only used from the growth rings formed at ages 6, 8 and 10 years. From these rings, three measurements were used and these were average density, minimum density and density differential, which was the difference between the maximum and minimum density within each measured ring. A total of 471 trees were sampled with 5 trees being sampled per family per site. Further details about the methods are given in Evans *et al.* (2000).

4.2.2 Estimation of genetic parameters

Variances, covariances, correlations and errors for each site and each trait were estimated simultaneously by fitting a multivariate multisite model. Multivariate

analyses use information more efficiently and can improve the precision of genetic parameters when selected subsets of data are used (Dieters *et al.* 1999). An example of their use is shown and discussed in Apiolaza and Garrick (2001). Multivariate-multisite models allow all genetic correlations to be calculated directly, and use appropriate variance-covariance matrices for each site. These models treat measurements on different sites as different traits. Analyses were done using ASREML (Gilmour *et al.* 1999), and the model fitted was:

$$Y = \mu + SITE + REP + FAM(SITE) + \varepsilon \quad (4.1)$$

where Y is a vector of data for each trait; μ is the mean for each trait; SITE are the site effects for each trait fitted as a fixed factor; REP are within site replicate effects for each trait fitted as a fixed factor; FAM(SITE) are within site family effects for each trait fitted as a random factor; and ε is a vector of residuals for each trait. Full inter-trait and inter-site variance and covariance matrices were fitted for the family and residual effects.

A second model was fitted to determine the importance of genotype by environment interactions and to estimate genetic correlations and heritabilities when data was pooled across sites. This was a multivariate combined site model. Error variances for each trait were all similar and therefore adjusting to a constant error variance was not considered necessary. The analysis was also done using ASREML and the model fitted was:

$$Y = \mu + SITE + REP + FAM + FAM.SITE + \varepsilon \quad (4.2)$$

where Y, μ, SITE, REP and ε are as previously defined; FAM are across site family effects fitted as a random factor; and FAM.SITE are site by family interaction effects fitted as a random factor. The model terms FAM and ε included an inter-trait variance and covariance matrix pooled across sites.

Heritabilities, site means and their standard errors were calculated using ASREML. Heritabilities for the individual site and multisite analyses were calculated as shown in models 4.3 and 4.4 respectively.

$$h^2 = \sigma^2_f / r\,(\sigma^2_f + \sigma^2_e) \quad (4.3)$$

$$h^2 = \sigma^2_f / r\,(\sigma^2_f + \sigma^2_{f.s} + \sigma^2_e) \quad (4.4)$$

Where h^2 is narrow sense heritability; σ^2_f, $\sigma^2_{f.s}$ and σ^2_e are, respectively, variance components for FAM, FAM.SITE and ε estimated in the models above; and r is the coefficient of relationship. The coefficient of relationship used was 0.4 which assumes a selfing rate of approximately 30% (Griffin and Cotterill 1988). However, more recent studies have suggested that a 30% selfing rate may be at

the upper end of measured values for *E. nitens* (Grosser *et al.* 2001) and therefore there is a risk that heritabilities may be slightly inflated.[vii]

4.2.3 Estimation of genetic gains

Genetic gains for diameter, basic density, cellulose, collapse, and appearance board grades were estimated under five selection strategies. This was done in a three-step process. Firstly, individual tree breeding values were calculated for diameter, basic density, cellulose and collapse. Secondly, for each selection strategy, individual tree index values were calculated and the average breeding values of a selected population were calculated. And thirdly, the assortment of appearance board grades was estimated using breeding values for collapse.

Calculation of breeding values

Individual tree breeding values were calculated by fitting the following multivariate model using ASREML:

$$Y = \mu + SITE + REP + TREE + FAM.SITE + \varepsilon \quad \textbf{(4.5)}$$

Where Y, μ, SITE, REP, FAM.SITE and ε are as previously defined and TREE are the individual tree breeding values (additive genetic) for diameter, basic density, cellulose and collapse. The terms TREE and ε included inter-trait variance and covariance matrices pooled across sites. Correlations were fixed to values calculated in model 4.2 and a coefficient of relationship of 0.4 was assumed for calculating additive variances.

Selection of trees and estimation of gains

Five selection strategies were evaluated, with different sets of economic weights being applied for each strategy (Table 4.3). The weights describe the relative importance of a standard deviation unit of that trait. The growth index (1) maximises volume per ha. The wood chip index (2) maximises profit per hectare from wood chip production. Index values are based on those of Borralho *et al.* (1993) with weights converted to standard deviation units. The kraft pulp index (3) maximises profit per hectare for unbleached kraft pulp production. Index values are from Greaves *et al.* (1997a) and have also been converted to standard deviation units. The collapse index (4) minimises collapse, or maximises recovery of high grade appearance timber. The appearance sawlog index (5) represents an index that maximises profit per ha when selling appearance grade products and places equal weights on maximising volume and minimising collapse. For this index, weights are not true economic weights because no

[vii] See section 3.2.2 for more details.

economic information has been used – they are estimates used to demonstrate, in simple terms, the effect of using collapse as part of multitrait selection.

Table 4.3. Economic weights (in standard deviation units) for each selection index.

Index	D	BD	CEL	COL
1. Growth	1	0	0	0
2. Wood chip	1	1	0	0
3. Kraft pulp	3	3	1	0
4. Collapse	0	0	0	1
5. Appearance sawlog	3	0	0	2

Individual tree index values were calculated for each selection strategy as:

$$I = BV_D.W_D/\sigma_D + BV_{BD}.W_{BD}/\sigma_{BD} + BV_{CEL}.W_{CEL}/\sigma_{CEL} + BV_{COL}.W_{COL}/\sigma_{COL} \quad (4.6)$$

Where I is a unitless index value, BV is the breeding value for each trait (see Table 4.2 for definition of subscripts), σ is the additive genetic standard deviation for these traits; and W is the economic weight for each trait. The economic weights used for each index are shown in Table 4.3.

For each selection strategy, trees were sorted by the index value (I) and the average breeding values of the top 60 trees calculated for diameter, basic density, cellulose content and collapse. This represents a selection intensity of 5% and simulated selecting 20 trees for a clonal seed orchard with a restriction that no family be represented by more than two individuals. The average value of the top 60 trees was expressed as a percentage gain over the unselected population

Estimation of board grades

The assortment of appearance grade board grades was estimated for each selection strategy. After knots, checking has been identified as the major source of appearance product degrade in 25 year old *E. nitens* with other factors, such as kino and splitting, being small (Waugh and Yang 1994). Since pruning is standard practice for *E. nitens* sawlog plantations (Neilsen and Pinkard 2000) knots are not a factor and, in this analysis, it is assumed checking is the primary factor determining board grade. Therefore checking was used to predict board grade. This was done by, firstly, predicting checking from collapse; and secondly, predicting board grades using these checking values.

Breeding values for checking were predicted as:

$$BV_{CHECK} = BV_{COL} \cdot r_g \quad (4.7)$$

Where BV_{CHECK} are individual tree breeding value for board checking in units of genetic standard deviation; BV_{COL} are breeding value for collapse measured on core samples and calculated in model 4.5, also in units of genetic standard deviation; and r_g is the genetic correlation between board checking and core

collapse. The genetic correlation between board checking and core collapse is unknown but was assumed to be 0.7 for this analysis. By assuming this imperfect correlation it is recognised that collapse will not explain all variation in checking.

Board grades were defined according to the groupings shown in Table 4.4. This grading system was used by Waugh and Yang (1994) to grade plantation grown *E. nitens* in a Tasmanian saw milling study. The percentages of product out-turn for each grade, which is also shown in Table 4.4, are the out-turns estimated by Waugh and Yang assuming branches have been removed. This grading system was developed by Waugh and Roza (1991) as a visual grading system for young native forest eucalypts. It grades on 10 criteria, which include surface checks, internal checks, green knots, holes, kino, spring/bow, sapwood and end splits. However, for reasons discussed above, only surface checks and internal checks were used to define board grades in this current study. The product out-turns shown in Table 4.4 are used to describe the baseline and it is assumed this data represents a typical rotation age *E. nitens* pruned plantation.

Table 4.4. Definitions of appearance board grades.

Board grade [i]	Surface checks [i] (mm per m^2)	Internal checks [i] (no. per 50 cm^2)	No. boards in grade (%)[ii]	Range [iii] (SD units)
1. Joinery	250	1	40	<-0.25
2. Select	300	1	26	-0.25 – 0.41
3. Standard	1000	3	14	0.41 – 0.84
4. Utility	2000	6	20	>0.84

i) Board grades and definitions of checking after Waugh and Roza (1991).

ii) Percentage of product out-put measured by Waugh and Yang (1994) for 25 year old *E. nitens*.

iii) Taken from table of cumulative probabilities of the standard normal distribution. For example, for joinery grade Pr ($z < -0.25$) = 40%.

Board grades were defined in standard deviation units using the frequencies in each grade given by Waugh and Yang (1994). The ranges of values appropriate for those frequencies are shown in Table 4.4 and were taken from tables of the cumulative probability of the standard normal distribution. Values for BV_{CHECK} (calculated in equation 4.7) were then converted to a board grade and, for each selection strategy, the frequency distribution calculated.

4.3 RESULTS

4.3.1 Site differences

There were statistically significant differences between sites for all traits (Table 4.5). Growth rates on all sites were good and total volumes were predicted to be

235, 226 and 268 m^3 ha^{-1} for Dial, Gog and Kamona respectively.[viii] Basic density and cellulose content were highest at Gog, and collapse at this site was lowest. For basic density and cellulose, differences between Gog and other sites were about 4 to 5% but for collapse the differences were about 20%.

Table 4.5. Least square trait means (± standard error) for each site.

Trait	Dial	Gog	Kamona
D (cm)	18.4 ± 1.0	20.8 ± 1.0	23.6 ± 1.1
BD (kg m^{-3})	441 ± 5	470 ± 6	450 ± 5
CEL (%)	40.3 ± 0.3	43.0 ± 0.3	41.3 ± 0.2
COL (% shrinkage)	18.6 ± 1.7	13.4 ± 1.7	16.5 ± 1.7

4.3.2 Heritabilities

Heritabilities for each site and for a combined site analysis are shown in Table 4.6. In a combined site analysis, all traits had heritabilities that were moderately high (ranging from 0.40 to 0.56) and for all traits except diameter there was significant between site variation in heritabilities. Basic density and cellulose content had very high heritabilities on some sites (Gog and Kamona) and, on these sites, it appears most variation is explained by additive genetic variance.

Table 4.6. Heritabilities (± standard error) for each site and all sites combined.

Trait	Dial	Gog	Kamona	All sites
D	0.37 ± 0.12	0.45 ± 0.13	0.32 ± 0.12	0.40 ± 0.10
BD	0.50 ± 0.16	0.96 ± 0.18	0.63 ± 0.17	0.53 ± 0.13
CEL	0.52 ± 0.21	0.86 ± 0.20	1.05 ± 0.21	0.56 ± 0.15
COL	0.23 ± 0.11	0.48 ± 0.15	0.61 ± 0.17	0.38 ± 0.10

4.3.3 Correlations

Genetic correlations for the combined site analysis are shown in Table 4.7. Favourable and strong genetic correlations occurred between diameter and cellulose and between basic density and collapse, and these were stable across sites. Adverse and moderately strong correlations occurred between diameter and basic density, diameter and collapse, basic density and cellulose, and between cellulose and collapse. Correlations between diameter and collapse, basic density and collapse and between diameter and cellulose were stable across sites, but for all others site variation was significant. For example, genetic correlations for cellulose and collapse varied between 0.21 and 0.85 and genetic correlations between diameter and basic density varied from between –0.16 and –0.77.

[viii] Volumes were predicted using Farm Forestry Toolbox (Private Forests Tasmania 2001) from mean dominant height data and basal area data.

Table 4.7. Genetic correlations (r_G) with standard errors above diagonal and phenotypic correlations (r) below diagonal.

Trait	D	BD	CEL	COL
D		-0.57 ± 0.15	0.79 ± 0.10	0.75 ± 0.10
BD	-0.11		-0.45 ± 0.18	-0.75 ± 0.11
CEL	0.32 **	0.11 *		0.54 ± 0.16
COL	0.47 **	-0.36 **	-0.02	

** = Significantly different from zero at P<0.01; * = Significantly different at P<0.05.

Phenotypic correlations between traits are shown in Table 4.7. Correlations between most traits were either weak or not significantly different from zero. Correlations were also measured separately for each site, and were essentially the same as for the combined site data. The strongest correlations were those for collapse with diameter (r = 0.47) and for collapse with basic density (r = –0.36). A multivariate relationship of collapse with diameter and basic density had a better correlation (r = 0.56), although this relationship still only explained 31% of total variation and therefore appears of limited practical value.

Genetic and phenotypic correlations between collapse and wood density measured using x-ray densitometry (SilviScan-2) are shown in Table 4.8. It is thought that collapse may be influenced by low earlywood density or high differences between earlywood and latewood density rather than density averaged across growth rings (Chafe *et al.* 1992, Yang 1996). However, in this study these measures of density were not good predictors of collapse. Correlations between collapse and the minimum density within a ring age were lower than those calculated using bark to bark averages (compare Tables 4.7 and 4.8) and correlations between collapse and the density differential within a ring were significantly lower than for other measures of density.

Table 4.8. Genetic correlations (r_G) and phenotypic correlations between collapse and wood density measured by x-ray densitometry (SilviScan-2).

Age	Density measure	r_G ± se	r [i]
6	Average	-0.57 ± 0.21	-0.25 **
	Minimum	-0.28 ± 0.25	-0.19 **
	Differential	-0.33 ± 0.25	-0.14 **
8	Average	-0.58 ± 0.19	-0.32 **
	Minimum	-0.57 ± 0.22	-0.22 **
	Differential	-0.24 ± 0.28	-0.18 **
10	Average	-0.61 ± 0.19	-0.28 **
	Minimum	-0.63 ± 0.21	-0.19 **
	Differential	- [ii]	-0.09 *

i) ** = significantly different from zero at P<0.01; * = significant at P<0.05.

ii) r_G could not be measured because genetic variation was close to zero.

4.3.4 Genotype by environment interaction

No genotype by environment interaction was present for diameter and collapse. For these traits family by site variance was zero (Table 4.9) and genetic correlations between sites were very high (Table 4.10). Genotype by environment interactions for basic density and cellulose content were significant but relatively small. Family by site variance contributed about 5% of total variance for these traits (Table 4.9) and genetic correlations between sites ranged between 0.67 and 0.92 (Table 4.10). However, for both these traits the interactions appear of no practical significance. Basic density interactions appear caused by minor rank changes in many families and no families had large differences in ranking between sites. Excluding the most interactive families did not substantially alter the size of interactions. Cellulose content interactions appear to be caused by scale effects. This occurs where genetic expression on one site is much stronger than other sites. After weighting cellulose data by the site standard deviation, family by site variance was less than 1%.

Table 4.9. Variance components and heritabilities (± standard error) for combined site analyses.

Trait	σ^2 family	σ^2 family.site [i]	σ^2 error	h^2
D (cm)	5.7 ± 1.6	0 ± 0	29.9 ± 1.3	0.40 ± 0.10
BD (kg m^{-3})	200 ± 61	59 ± 24	673 ± 36	0.53 ± 0.13
CEL (% kg kg^{-1})	0.38 ± 0.11	0.01 ± 0.04	1.22 ± 0.09	0.56 ± 0.15
COL (% shrinkage)	7.0 ± 2.1	0 ± 0	39.2 ± 2.1	0.38 ± 0.10

[i] ASREML calculated small negative family by site variances for D and COL and therefore the analysis was redone with these values fixed to zero.

Table 4.10. Genetic correlations (± standard error) between sites.

Trait	Dial & Gog	Dial & Kamona	Gog & Kamona
D	1.09 ± 0.10	0.93 ± 0.13	1.14 ± 0.12
BD	0.73 ± 0.15	0.67 ± 0.19	0.92 ± 0.11
CEL	0.77 ± 0.23	0.91 ± 0.19	0.89 ± 0.15
COL	1.01 ± 0.18	1.00 ± 0.25	0.98 ± 0.16

4.3.5 Genetic gains

The target criterion for appearance grade products is assumed to be select grade or better, and the percentage of product meeting this board grade is predicted to change substantially under different selection strategies (Table 4.11). The worst selection strategy is to select for diameter alone. This strategy would result in a substantial drop in wood quality, with only 8% of boards making select grade or better. Selecting on a wood chip index (i.e. diameter and basic density) appears to maintain appearance grade wood quality at its current level, and achieve gains in growth and basic density. Selecting on a kraft pulp index gives a similar result,

with similar proportions of boards making select grade or better. However, under this selection strategy it appears that recovery for the highest grade will reduce.

Good genetic gains in reducing the effects of collapse can be made when selecting directly for this trait alone (Table 4.11) with a 35% decrease in the amount of collapse predicted. This is expected to result in all boards meeting the top appearance grade. However, these gains come with a large sacrifice in growth and diameter is predicted to fall by 18%. Reasonable improvements in both growth and collapse can be obtained using the appearance sawlog index, which selects for both diameter and collapse. Predicted improvements are a 9% gain in growth and a 7% reduction in collapse (Table 4.11). Importantly, this gain in collapse is predicted to give a substantial improvement in appearance grade board quality, with 93% of boards predicted to make select grade or better.

Table 4.11. Genetic gains (% of mean value) using different selection strategies. For COL positive numbers are adverse (increased severity) and negative numbers favourable (reduced severity).

Index	Genetic gains (%)				Board grades (%)			
	D	BD	CEL	COL	Joinery	Select	Stand.	Utility
Current standard	0	0	0	0	40	25	12	23
1. Growth [i]	20	-4	3	32	0	8	28	63
2. Wood chip [ii]	8	3	1	-3	40	35	20	5
3. Kraft pulp [ii]	13	1	2	4	20	48	23	8
4. Collapse [iv]	-18	6	-2	-35	100	0	0	0
5. Appearance sawlog [v]	9	2	2	-7	40	53	7	0

[i] Selecting for D only.

[ii] Economic weights to maximise profit per ha from production of wood chips. Data and methods are from Borralho *et al.* (1993). Weights were converted to standard deviation units and relative weights were 1 each for D and BD.

[iii] Economic weights to maximise profit per ha from production of unbleached kraft pulp. Weights are from Greaves *et al.* (1997a) and have been converted to standard deviation units. Relative weights are 3, 3 and 1 for D, BD and CEL respectively.

[iv] Maximise recovery of appearance grade products (i.e. selecting for COL only).

[v] Hypothesised economic weights to maximise value selling appearance grade sawlog products. Relative weights, in standard deviation units, are 3 for D and 2 for COL.

4.4 DISCUSSION

Collapse and checking are fundamental problems for the production of sawn timber for many eucalypt species (Jacobs 1979) and it appears that *E. nitens* is a species susceptible to checking (Waugh and Yang 1994, McKenzie *et al.* 2002a). In addition, there is evidence that some sites will express this problem more severely than other sites (Shelbourne *et al.* 2002). Checking appears to be more severe in the high value lower pruned log (Raymond and Savage, unpublished data) and thus is likely to have a severe impact on the economics of growing for appearance products. The silvicultural regime required for sawlog production (i.e.

prune, thin and grow for a longer rotation) is a high cost regime and is dependent on high product prices to be profitable. If checking is a major cause of downgrade in end product quality, as it appears from the grading system defined by Waugh and Roza (1991), then inclusion of this trait into *E. nitens* breeding programs would be a priority.

This study indicates that tree breeding can be used as a tool to manage collapse and checking. However, before a breeding plan can be implemented there are two questions to be answered. These are; firstly, 'what is the best selection trait?' and secondly, 'what economic weight do you apply?'

4.4.1 Selection traits

An essential criterion for a selection trait is that it be correlated with the breeding objective trait. In this study, it has been assumed that tangential collapse of a wood core (the selection trait) is moderately correlated ($r_g = 0.7$) with board checking (the objective trait). There are two aspects to this assumption. The first is that collapse of a core is related to collapse of the pruned (or lower) log, and a study by Raymond and Savage (unpublished data) suggests that for both *E. nitens* and *E. globulus* this is a valid assumption. The second is that collapse is related to checking. For eucalypts in general it is known that collapse is a major cause of checking but not the only cause; some checking can be attributed to other factors such as tension wood (Hillis 1978, Jacobs 1979, Chafe *et al.* 1992). In this study it has been assumed that most checking in *E. nitens* is caused by collapse, but an allowance for other factors was made by using an imperfect genetic correlation between collapse and board checking ($r_g = 0.7$). The assumption that collapse is the main cause is supported by the study of McKenzie *et al.* (2002b), where tangential collapse measured on *E. nitens* discs was well correlated with checking on butt log boards ($r = 0.73$), and also by the study of Ilic (1999) where collapse measured on *E. regnans* boards was correlated with checking measured on the same boards ($r = 0.68$). Importantly, this latter study noted that low levels of collapse were always associated with low numbers of checks.

Another important criterion for a selection trait is that it can be assessed in a cheap and non-destructive fashion. Measuring tangential collapse on a wood core meets this standard. If cores are already being taken for basic density sampling, then the cost will be less than AU$0.50 per tree and including this assessment in a breeding program could be done with only a 5% increase in the basic density sampling cost. The method is also very simple. The major potential cause of inconsistent results is non-uniform drying and this can happen if cores are allowed to begin drying at room temperature before being put into the oven. The problem can be avoided by ensuring cores are always oven dried from the saturated state. Other traits, such as density variation or minimum density, have been suggested as selection traits for collapse (Chafe *et al.* 1992, Yang 1996) but these are more

expensive to measure and imperfect predictors. Collapse is caused by thin cell walls and presumably measurements of density, even very specific measures, are not perfect measures of this property.

4.4.2 Economic weights for appearance sawlogs

A fundamental question for a forest grower planning to sell appearance grade products is: 'how should selections be made?' This question is particularly important because of the high cost silvicultural regime required. The wrong tree breeding decisions may result in wood quality being unsuitable for the appearance grade market and this may jeopardise the profitability of these plantations.

Economic weights for traits are chosen to maximise profitability and are usually made after an economic evaluation of production processes and market prices. This has been done for kraft pulp production (e.g. Borralho *et al.* 1993, Greaves *et al.* 1997a) and these examples are good case studies for the methodology. However, this has not been done for the production of appearance grade timber and cannot be done at present because the industry is new and markets for this wood are not established. Therefore there are no strong market signals to forest growers. Furthermore, these types of decisions are complex for solid wood growers because they are usually intending to produce a range of products from the same trees. It is important that decisions that aim to improve the quality of appearance products do not lead to a degradation of product quality for alternative markets, particularly for wood chips and pulp production, where there are established markets. Therefore in this analysis some typical industry indices were evaluated and are compared to a 'best guess' appearance grade sawlog index.

An important finding of this study is that appearance grade wood quality is predicted to decline markedly when selecting for growth alone. This would virtually exclude the possibility of selling logs to the joinery market. Under this strategy, plantations that had been silviculturally managed to produce for this market (i.e. pruned, thinned and grown on a 20 year rotation) would probably make a financial loss, despite genetic gains in growth. This is because high product prices are necessary to pay for the investment in such regimes (see Candy and Gerrand 1997).

Selecting on a wood chip index or kraft pulp index appears to be a suitable selection strategy if appearance grade wood quality is currently adequate. Checking does not appear to get any worse and gains are made in growth and basic density. Therefore, this strategy would provide increased profitability through decreased growing costs (i.e. improved productivity) and increased value for the sale of wood chips without excluding the appearance grade market.

Selecting only to reduce collapse would probably be an uneconomic proposition for a forest grower under present cost structures. Although big reductions are

predicted for checking, it comes at a high cost in terms of growth rate. An 18% drop in diameter would result in a site that previously had a productivity of, say, 25 m^3 ha^{-1} $year^{-1}$ falling to less than 20 m^3 ha^{-1} $year^{-1}$. Site productivity is the most sensitive variable to eucalypt sawlog plantation profitability and, in a study in Tasmania, sawlog plantations were uneconomic when site productivity was low (Candy and Gerrand 1997). In addition, selecting in this way would increase the growing cost of wood and limit options for selling other products. Therefore, this is not a selection strategy that a grower would be likely to adopt.

Reasonable improvements in growth and reductions in the amount of checking can be obtained simultaneously using an appearance sawlog index. Importantly, the shift in checking under this strategy is predicted to be adequate to ensure most boards meet the standards for the joinery market (that is select grade or better). This strategy also provides reasonable gains in pulpwood quality (basic density and cellulose content) and therefore does not appear to exclude the sale of other products from the same trees. Selecting for collapse appears to give much better improvements in appearance board quality than when selecting simply for basic density. Therefore sawlog growers should select directly for this trait rather than assuming that selecting for basic density will be suitable.

4.5 CONCLUSION

Collapse is a trait that should be included in breeding programs if logs are to be sold for appearance grade products. Collapse is under moderate to high genetic control and is not influenced by genotype by site interactions. It has strong and favourable genetic correlations with basic density but strong and adverse correlations with diameter growth. Tangential collapse can be measured on 12 mm increment cores easily and at low cost. If basic density is being measured, collapse can be assessed at very little additional cost.

The percentage of product in different appearance board grades is predicted to change substantially with different selection strategies. If selecting for diameter alone, a large increase in checking is predicted and very few boards are expected to be acceptable for the joinery market. Selecting on a wood chip or kraft pulp index is expected to cause minimal changes in checking and therefore this is a reasonable option if current wood quality is acceptable for the appearance grade market. If it is required to lower the incidence of checking, and evidence from other studies suggests this will be the case, then an index including diameter and collapse is recommended. Selecting in this way is predicted to improve growth and decrease the incidence of checking to a point where most boards will be suitable for the joinery market.

CHAPTER 5

5. Breeding for Resistance to Wood Decay

5.1 INTRODUCTION

Eucalyptus nitens has many of the characteristics required for high quality structural and appearance products but, because it retains dead branches, knots are the major cause of downgrade in product quality (McKimm *et al.* 1988, Waugh and Yang 1994). Therefore pruning regimes have been developed to produce high value products (Neilsen and Pinkard 2000). Green branch pruning has been found to be necessary to reliably produce clear timber. This is because pruning dead branches carries a high risk of branch stubs becoming trapped in the bark and, instead of being occluded, they are drawn outwards by the growing stem leaving a kino trace (Wardlaw and Neilsen 1999). Thinning is also necessary to produce high quality structural and appearance products from *E. nitens* plantations. Final stockings of 200 to 300 stems per ha provide growth advantages and, under this regime, 50 cm logs are expected with a 20 year rotation (Neilsen and Pinkard 2000, Medhurst and Beadle 2000). Good growth responses are also possible after waste thinning at age 5 years, although commercial thinnings for pulpwood at age 10 to 12 years is preferred because of better financial returns (Candy and Gerrand 1997).

Wood decay is a major risk to the profitability of *E. nitens* veneer and sawlog plantations and pruning, thinning and site are factors that influence the incidence of decay. Green branch pruning is the most important factor and carries a high risk of initiating stem decay as it provides an entry point for decay organisms. In a study over five Tasmanian sites, the probability of uncontained decay in pruned trees was found to be approximately 30% higher than that of unpruned trees (Mohammed *et al.* 2000). The risk of decay increases when larger branches are pruned and when branch diameter is greater than 30 mm the risk is considered unacceptable for commercial plantations (Wardlaw and Neilsen 1999, Mohammed *et al.* 2000). Thinning also carries a risk of decay, although this risk appears less than that of pruning. Operational thinning trials in *E. regnans* regrowth caused damage that led to decay in between 9 to 16% of retained trees (White and Kile 1991). Wounds to the butt were, by far, the most frequent type of wound. Similar levels of damage were found in an operational thinning of 11 year old *E. globulus* in Tasmania (Gerrand *et al.* 1997). Site is also an important

factor in explaining the incidence of decay both before and after pruning. Across five Tasmanian sites, the probability of unpruned and pruned trees developing uncontained decay outbreaks varied between 0.03 to 0.44 and 0.13 to 0.76 respectively (Mohammed *et al.* 2000). Decay problems appeared more severe on highly productive sites, and the site with the lowest decay incidence was considered marginal for solid wood production due to low productivity.

Mechanisms of tree response to decay have been described and theories range from compartmentalisation of decayed wood by physical barrier zones (Shigo and Marx 1977) to more dynamic reaction zones where a range of tree responses can continue to stop the spread of decay (Pearce 1996). Responses in *E. nitens* have been studied in detail by Barry *et al.* (2000), who found that many properties of *E. nitens* reaction zones were different from other angiosperms. Unlike other eucalypts, *E. nitens* does not form kino barriers. The onset of decay in *E. nitens* is influenced by a complex set of internal xylem defence mechanisms such as the accumulation of phenolics, formation of tyloses, decreases in potassium levels and decreases in pH. These mechanisms form the reaction zone and represent the tree's response to attack. The successful exclusion of decay most probably represents the success of a number of tree responses in preventing the establishment of decay organisms and therefore resistance to decay could be considered the amalgamation of a number of genetic traits. These responses are thought to be different on different sites (Barry 2001) which would cause genotype by environment interactions in the direct measurement of decay incidence. Barry *et al.* (2000) found the xylem defence mechanisms had effectively contained decay for up to 9 years. However, they emphasise that their effectiveness for the life of the crop remains to be seen.

Management of *E. nitens* sawlog plantations to minimise the risk of decay is critical. This is principally done by managing branch size and ensuring trees with branches greater than 30 mm are not pruned (Neilsen and Pinkard 2000). Avoiding poor pruning practices has also been found to be important because damage due to pruning will increase the risk of decay (Gerrand *et al.* 1997, Mohammed *et al.* 2000). Fungicides and sealants gave some improvement but their success was variable and they were not considered cost-effective (Mohammed *et al.* 2000).

Tree breeding is, potentially, another tool that can be used to manage wood decay. However, little published information is available on the extent to which wood decay is under genetic control. White *et al.* (1999) measured the discolouration associated with artificial wounds in *E. nitens* and reported heritabilities of 0.13 to 0.17, but warned these estimates had high standard errors and were based on small sample sizes. Genetic variation in the susceptibility to decay or defect is reported for other hardwood species such as *Liquidambar styraciflua* L., *Populus deltoides*

Bartr. (Garrett *et al.* 1979), *Populus tremuloides* Michx. (Weingartner and Basham 1985), and *Populus nigra* x *P. mazimowiczii* clones (Noh *et al.* 1986). There appears to be no record of this trait being part of breeding programs.

This study evaluates tree breeding as a tool to manage wood decay in *E. nitens*. The aims were to; firstly, calculate the degree of genetic control for decay; secondly, determine relationships between decay and other traits; and thirdly, assess the potential of tree breeding to change the incidence of decay in plantations.

5.2 MATERIAL AND METHODS

5.2.1 Trial establishment

The genetic material was open pollinated progeny of 40 native forest families from the Toorongo Plateau in the central highlands of Victoria and the location is described in Pederick (1979). Mother trees were growing as a pure stand in an open forest and stem diameters ranged from 35 to 110 cm.

Progeny trials were established in 1984 on three sites in northern Tasmania, all with good soil fertility and good productivity (Table 5.1). Stocking at planting was 1111 trees ha^{-1} (3 m by 3 m spacing) and survival at age 12 years was 81%. The trial design was a randomised complete block with single tree plots and 16 replications per site.

Table 5.1. Location and description of trial sites.

	Dial	Gog	Kamona
Latitude (South)	41° 10'	41° 29'	41° 08'
Longitude (East)	146° 04'	146° 23'	147° 40'
Altitude (m)	100	300	160
Rainfall (mm per year)	1060	1200	1150
Mean maximum temp. warmest month (°C)	22.3	21.8	23.4
Mean minimum temp. coolest month (°C)	3.8	2.4	2.5
Site index (m) [i]	26.3	27.5	28.6
Parent material	mudstone	basalt	granite

[i] Site index is mean dominant height at age 15 years and was predicted using Farm Forestry Toolbox (Private Forests Tasmania 2001) after measuring the mean dominant height on each trial site.

5.2.2 Assessments

A total of nine traits were assessed as part of this study and Table 5.2 summarises the data for each trait. Growth was assessed by measuring diameter at breast height (1.3 m) at 12 years for all trees at all three sites. Branch size was assessed on all trees at age 6 years at the Dial and Gog sites. Assessment was done using a 6 point scale where 1 represented the largest branches on that site and 6 the

smallest branches. The largest and smallest branches on the site were determined visually in a preliminary pre-assessment.

Table 5.2. Description of data used in analyses.

Trait		Age (years)	Min.	Mean	Max.	SD	n
D	Dbh age 12 (cm)	12	10.1	21.1	40.4	6.0	1160
BD	Basic density (kg m^{-3})	12	362	451	568	31	841
CEL	Cellulose content (% kg kg^{-1})	13	38.0	41.5	45.4	1.4	545
EXT	Ethanol soluble extractives (%)	13	1.2	3.1	5.8	0.7	434
BR	Branch score (1 to 6) [i]	6	1	3.7	6	0.8	805
DEC_h	Incidence of heart-rot decay [ii]	13	0	0.29	1		347
DEC_w	Incidence of wounding decay [iii]	13	0	0.17	1		189
DIC_h	Incidence of heart-rot discolouration [ii]	13	0	0.61	1		347
DIC_w	Incidence of wound discolouration [iii]	13	0	0.32	1		189

[i] BR was measured at two sites (Dial and Gog). 1 = large branches and 6 = small branches.

[ii] DEC_h and DIC_h were measured at two sites (Dial and Kamona). No heart rot was present at the third site (Gog).

[iii] DEC_w and DIC_w were measured at one site (Gog). Incidence was very low at the other sites.

Basic density was measured at 12 years using a 12 mm diameter bark-to-bark core at a height of 0.9 m. Core sampling at this height has been shown to be a reliable predictor of whole tree values of basic density (Raymond and Muneri 2001, Chapter 2 of this thesis). Basic density was defined as oven-dry wood mass per unit volume of green wood, and was measured using the water displacement method (Hendrichs and Larson 1970; TAPPI 1989). Samples were taken from all sites and between 5 and 13 trees per family per site were randomly sampled (average of 8). Following an initial analysis, 11 trees were excluded due to high residuals (greater than 3 standard deviations from mean). These trees had low diameters, very little diameter increment between 6 and 12 years, and very high density. The number of trees sampled and range of values are shown in Table 5.2.

Crude cellulose content (g cellulose per wood dry mass) was assessed at 13 years using a 12 mm bark to bark core taken at a height of 0.9 m. Cores taken at this height are known to be reliable predictors of whole tree cellulose content (Chapter 2 of this thesis). Cores were dried at 27°C, ground and assayed using the method of Wallis *et al.* (1997). Five trees were randomly sampled per family from each site. More details of the sampling and analysis are given in section 3.2.1.

Methanol-soluble extractives content (g extractives per wood dry mass) was measured at 13 years using the same ground wood samples used to measure cellulose content. Samples were assayed using a Soxhlet extractor with approximately 2.5 g of wood meal. The extraction process ran until the solvent was clear, which took between two and four hours, and then the weight loss of the

wood sample was measured. Five trees were randomly sampled per family from Dial and Gog and approximately four trees per family were sampled at Kamona.

Core samples used to assess of cellulose and extractives contents were collected approximately one year after the basic density cores, with the second core being taken 10 cm directly above the first core. The presence of both discolouration and decay was noted in the second set of cores. The extent of both discolouration and decay was measured as it was thought this might be important in explaining aberrant cellulose data (decayed parts of the core were removed prior to preparing samples for chemical analysis). The proportion of the core that was decayed or discoloured was measured after cores had been soaked in water, but subsequently this data was converted to incidence data (i.e. presence or absence). Decay was considered present when lighter coloured tissue with obviously softer texture was seen, and discolouration present when the wood was obviously darker but not detectably softer than adjacent clear wood. Decay and discolouration typically occupied two distinct zones within the stem cross section. One zone was in the sapwood, arising from the core sampling. Decay and discolouration in this zone was termed wound-rot. The other zone was in the heartwood at the centre of the core. Decay and discolouration in this zone was termed heart-rot. Wound-rot and heart-rot were assessed separately. Destructive sampling, which was done as part of another study (see section 2.2.2), provided an opportunity to examine the spread of the wounding decay. In a sample of 25 trees at Gog, wound-rot was verified to be the result of wounding that occurred when the first core was taken and the spread was always localised. The time intervals between the first core (the wounding) and the second core (the assessment) were 10, 12 and 16 months at Dial, Gog and Kamona respectively.

5.2.3 Estimation of phenotypic relationships

Phenotypic correlations involving decay could not be calculated directly because wound-rot and heart-rot were assessed as binomial variables (presence or absence) and the other traits as continuous variables. To overcome this, the continuous data for each variable was divided into five equal categories and the incidence of wound-rot or heart-rot was determined for each category. If the incidence of wound-rot or heart-rot showed systematic changes across the categories for any trait, a relationship between the trait and decay was inferred. Phenotypic correlations between diameter, basic density, and cellulose content are presented and discussed in Chapter 3 of this thesis.

5.2.4 Estimation of genetic parameters

The traits DEC_h, DEC_w, DIC_h and DIC_w were analysed as presence or absence data. A binomial distribution was assumed with a probit link function and the analyses were done using ASREML (Gilmour *et al.* 1999). Models used for the

analysis of individual sites separately and for sites combined are shown below as models 5.1 and 5.2 respectively.

$$Y = \mu + REP + FAM + \varepsilon \quad \textbf{(5.1)}$$

$$Y = \mu + SITE + REP + FAM + FAM.SITE + \varepsilon \quad \textbf{(5.2)}$$

where Y is a vector of data for each trait; μ is the mean; REP are within site replicate effects fitted as a fixed factor; FAM are either within site family effects (model 5.1) or across site family effects (model 5.2) fitted as a random factor; SITE are site effects fitted as a fixed factor; FAM.SITE are site by family interaction effects fitted as a random factor; and ε is a vector of residuals for each trait.

The traits D, BR, BD, CEL and EXT were analysed as continuous variables, also using ASREML, and two models were fitted. The first model (model 5.3) was a multivariate multisite model that estimated variances, covariances, correlations and errors for each site and each trait simultaneously. This model treated measurements on different sites as different traits and this model was used for the analysis of sites separately. The second model (model 5.4) was a multivariate combined site model that estimated variances, genetic correlations and genotype by environment interactions when data was pooled across sites. Error variances for each trait were all similar and therefore adjusting to a constant error variance was not considered necessary. The models were:

$$Y = \mu + SITE + REP + FAM(SITE) + \varepsilon \quad \textbf{(5.3)}$$

$$Y = \mu + SITE + REP + FAM + FAM.SITE + \varepsilon \quad \textbf{(5.4)}$$

where Y is a vector of data for each trait; μ is the mean for each trait; SITE are site effects fitted as a fixed factor; REP are within site replicate effects fitted as a fixed factor; FAM(SITE) are within site family effects fitted as a random factor; FAM are across site family effects fitted as a random factor; FAM.SITE are the site by family interaction effects fitted as a random factor; and ε is a vector of residuals for each trait. For model 5.3, full inter-trait and inter-site variance and covariance matrices were fitted for the family and residual effects. For model 5.4, the model terms FAM and ε included an inter-trait variance and covariance matrix pooled across sites.

Heritabilities, site means and their standard errors were calculated by ASREML. Heritabilities for single site analyses and multi-site analyses were calculated as shown in models 5.5 and 5.6 respectively.

$$h^2 = \sigma^2_f / r\,(\sigma^2_f + \sigma^2_e) \quad \textbf{(5.5)}$$

$$h^2 = \sigma^2_f / r\,(\sigma^2_f + \sigma^2_{f.s} + \sigma^2_e) \quad \textbf{(5.6)}$$

Where h^2 is narrow sense heritability; σ^2_f, $\sigma^2_{f.s}$ and σ^2_e are, respectively, variance components for FAM, FAM.SITE and ε estimated in the models above; and r is

the coefficient of relationship. The coefficient of relationship used was 0.4 which assumes a selfing rate of approximately 30% (Griffin and Cotterill 1988). However, more recent studies have suggested that a 30% selfing rate may be at the upper end of measured values for *E. nitens* (Grosser *et al.* 2001) and therefore there is a risk that heritabilities may be slightly inflated.[ix]

Genetic correlations between DEC_h and DEC_w could not be calculated directly since multivariate analyses were not possible for binomial data. Therefore genetic correlations were estimated by calculating correlations of family means (or more explicitly, proportion of trees within families with heart-rot or wound-rot), where family means were calculated using the model 5.2.

5.2.5 Estimation of genetic gains

Genetic gains for D, BD, CEL, BR, DEC_h and DEC_w were estimated under eight selection strategies. This was by calculating individual tree breeding values for each trait and then using these breeding values to estimate gains in selected populations under different selection strategies.

Individual tree breeding values were calculated by fitting the following model using ASREML:

$$Y = \mu + SITE + REP + TREE + FAM.SITE + \varepsilon \quad (5.7)$$

Where Y, μ, SITE, REP, FAM.SITE and ε are as previously defined and TREE are individual tree breeding values (additive genetic) for each trait. For the traits D, BD, CEL, and BR a multivariate model was fitted and the terms TREE and ε included inter-trait variance and covariance matrices pooled across sites. Correlations were fixed to values calculated in model 5.4 and a coefficient of relationship of 0.4 was assumed for calculating additive variances. The traits DEC_h and DEC_w were fitted as presence or absence univariate data and a binomial distribution was assumed with a probit link function.

Eight selection strategies were evaluated, each with a different set of economic weights (see Table 5.3). The weights describe the relative importance of a standard deviation unit of that trait. Growth indices (1 and 4) maximise the volume per ha. Wood chip indices (2 and 5) maximise profit per hectare from wood chip production. Index values were based on those of Borralho *et al.* (1993) with weights converted to standard deviation units. Kraft pulp indices (3 and 6) maximise profit per hectare for unbleached kraft pulp production. Index values are taken from Greaves *et al.* (1997) and have also been converted to units of standard deviation. The weights applied to wound-rot and heart-rot resistance are not true economic weights because no economic information has been used for

[ix] See section 3.2.2 for more details.

these traits – they are estimates applied here to demonstrate the effects on gains when using these traits as part of multi-trait selection. Individual tree index values were calculated for each of the eight selection strategies as:

$$I = BV_D.W_D/\sigma_D + BV_{BD}.W_{BD}/\sigma_{BD} + BV_{CEL}.W_{CEL}/\sigma_{CEL} + BV_{DECh}.W_{DECh}/\sigma_{DECh} + BV_{DECw}.W_{DECw}/\sigma_{DECw} \quad (8)$$

Where I is a unitless index value, BV is the breeding value for each trait (see Table 5.2 for definition of subscripts), σ is the additive genetic standard deviation for these traits; and W is the economic weight for each trait. The actual economic weights used for each index are shown in Table 5.3.

Table 5.3. Economic weights (in standard deviation units) for each selection index.

Index	D	BD	CEL	DEC_h	DEC_w
1. Growth	1	0	0	0	0
2. Wood chip	1	1	0	0	0
3. Kraft pulp	1	1	0.3	0	0
4. Growth + wound-rot resistance	1	0	0	0	2
5. Wood chip + wound-rot resistance	1	1	0	0	2
6. Kraft pulp + wound-rot resistance	1	1	0.3	0	2
7. Heart-rot resistance	0	0	0	1	0
8. Wound-rot resistance	0	0	0	0	1

For each selection strategy, trees were sorted by index value (I) and the average breeding values of the top 60 trees was calculated. This represents a selection intensity of 5% and simulated selecting 20 trees for a clonal seed orchard with a restriction that no family be represented by more than two individuals. The average value of the top 60 trees was expressed as a percentage gain over the unselected population

5.3 RESULTS

5.3.1 Site differences

There were statistically significant differences between sites for all traits (Table 5.4). Growth rates on all sites were good and total volumes were predicted to be 235, 226 and 268 m^3 ha^{-1} for Dial, Gog and Kamona respectively.[x] Basic density and cellulose content were highest at Gog where values were about 5% higher than the other sites. Site differences for extractives content appeared unrelated to other wood properties. Kamona had considerably lower extractives content than the other two sites. The incidence of heart-rot was highest at Kamona where 48%

[x] Volumes were predicted using Farm Forestry Toolbox (Private Forests Tasmania 2001) from mean dominant height data and basal area data.

of trees had heart-rot and lowest at Gog where no heart-rot was found. The incidence of wound-rot followed the reverse trend among sites to that found for heart-rot.

Table 5.4. Least square trait means (± standard error) for each site.

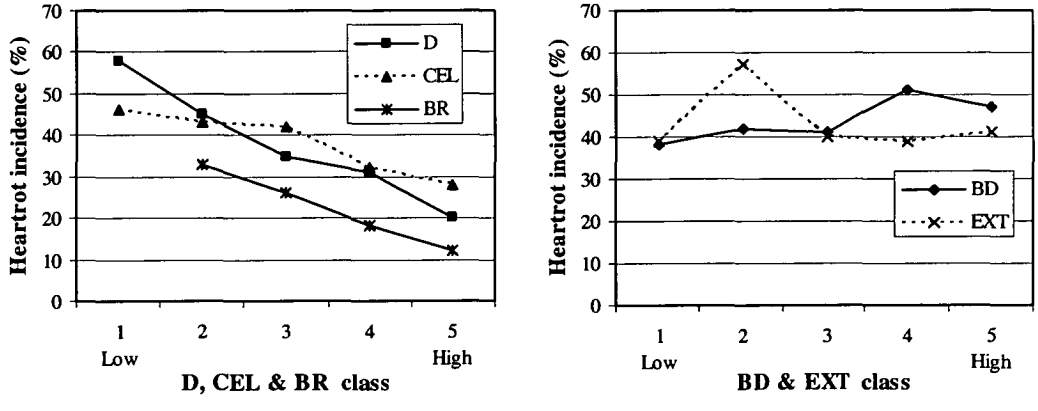
Trait	Dial	Gog	Kamona
D (cm)	18.4 ± 1.0	20.8 ± 1.0	23.6 ± 1.1
BD (kg m^{-3})	441 ± 5	470 ± 6	450 ± 5
CEL (% kg kg^{-1})	40.3 ± 0.3	43.0 ± 0.3	41.3 ± 0.2
EXT (%)	3.5 ± 0.1	3.2 ± 0.1	2.3 ± 0.1
BR (1 – 6 score)	3.7 ± 0.1	3.6 ± 0.1	
DEC_h (proportion) [i]	0.23 ± 0.04	0.00 ± 0.01	0.34 ± 0.04
DEC_w (proportion)	0.05 ± 0.04	0.17 ± 0.03	0.01 ± 0.01
DIC_h (proportion)	0.54 ± 0.04	0.01 ± 0.01	0.71 ± 0.04
DIC_w (proportion)	0.16 ± 0.02	0.32 ± 0.04	0.07 ± 0.02

i) Proportion containing decay or discolouration.

5.3.2 Phenotypic relationships

Phenotypic relationships between the incidence of heart-rot and other traits are indicated by the presence of systematic changes across the categories of those traits (Figure 5.1). The incidence of heart-rot appeared to be related to stem diameter, cellulose content and branching but unrelated to basic density and extractives content. Heart-rot decreased with increasing diameter, increasing cellulose content and smaller branches. Diameter appeared to be the most important variable, with 38% higher incidence of heart-rot in the small diameter class (<20 cm) compared with the large diameter class (>35 cm). For cellulose content, there was an 18% difference in the incidence of heart-rot in low cellulose content trees (<40%) compared with high cellulose content trees (>42%).

Figure 5.1. Incidence of heart-rot (% of trees affected) in each of five classes for stem diameter (D), basic density (BD), cellulose content (CEL), ethanol soluble extractives (EXT), and branch score (BR – high values represent small branches).



There were no apparent phenotypic relationships between the incidence of wound-rot and other traits. However, this may be due to the small sample assessed for wound-rot in this study (Table 5.2) combined with a low incidence of wound-rot.

5.3.3 Genetic parameters

Heritabilities for each site and for a combined site analysis are shown in Table 5.5. In a combined site analysis all traits except branching and discolouration had heritabilities that were moderately high (ranging from 0.35 to 0.75). The heritabilities for branching and discolouration were low (0.08 and 0.14) and not significantly different from zero. Heritabilities varied significantly between sites for all traits except diameter. This was primarily due to differences in additive genetic variance. Basic density, cellulose content and extractive content had very high heritabilities on some sites (Gog and Kamona) and, on these sites, it appears all variation is explained by additive genetic variance. Both the incidence of heart-rot decay and wound-rot had moderately high heritabilities.

Table 5.5. Heritabilities (± standard error) for each site and all sites combined.

Trait	Dial	Gog	Kamona	All sites
D	0.37 ± 0.12	0.45 ± 0.13	0.32 ± 0.12	0.39 ± 0.10
BD	0.50 ± 0.16	0.96 ± 0.18	0.63 ± 0.17	0.51 ± 0.13
CEL	0.52 ± 0.21	0.86 ± 0.20	1.05 ± 0.21	0.56 ± 0.15
EXT	0.22 ± 0.23	1.15 ± 0.21	1.29 ± 0.24	0.38 ± 0.14
BR	0.21 ± 0.09	0.07 ± 0.07		0.08 ± 0.06
DEC_h	0.63 ± 0.31		0.24 ± 0.22	0.41 ± 0.22
DEC_w		0.60 ± 0.35		
DIC_h	0.04 ± 0.22		0.21 ± 0.24	0.14 ± 0.13
DIC_w		0.20 ± 0.24		

Correlations of family means between heart-rot decay and wound-rot decay with other traits are shown in Table 5.6. There were no strong correlations between traits. The strongest and only statistically significant correlations were those between discolouration and decay for both wound-rot and heart-rot. Interestingly, there was no significant correlation between the incidence of heart-rot and wound-rot which suggests these are different traits.

Table 5.6. Correlations of family means between decay and other traits.

Trait	D	BD	CEL	EXT	BR	DEC_w	DIC_h	DIC_w
DEC_h	0.04	-0.10	-0.01	0.21	0.15	-0.23	0.45*	-0.29
DEC_w	0.18	-0.17	0.10	-0.06	0.05		-0.23	0.70*

* Significantly different from zero at $P<0.05$

Genetic correlations between the same traits on different sites are shown in Table 5.7. Correlations between diameter, basic density and cellulose content were

generally strong, and were discussed in Chapter 3. The correlation between heart-rot at Dial and Kamona was reasonably strong, suggesting these are the same traits on each site. Across site correlations for extractives content were moderate to low suggesting that the genetic expression of this trait is strongly influenced by site conditions and should be considered a different trait on each site.

Table 5.7. Genetic correlations (± standard error) between sites.

Trait	Dial & Gog	Dial & Kamona	Gog & Kamona
D	1.09 ± 0.10	0.93 ± 0.13	1.14 ± 0.12
BD	0.73 ± 0.15	0.67 ± 0.19	0.92 ± 0.11
CEL	0.77 ± 0.23	0.91 ± 0.19	0.89 ± 0.15
EXT	0.55 ± 0.36	0.16 ± 0.39	0.51 ± 0.18
BR	0.63 ± 0.48		
DEC_h [i]		0.77	
DIC_h [i]		0.14	

[i] DEC_w and DIC_h are correlations between family means.

5.3.4 Estimation of genetic gains

Good genetic gains in the resistance to decay could be obtained if selecting for only that trait (Table 5.8). If selecting only for wound-rot, a 46% gain was predicted, which represents a shift in decay incidence from say, 0.50 to 0.27. Similarly, if selecting only for heart-rot, the gain was predicted to be 38%, which represents a shift in incidence from 0.50 to 0.31.

Table 5.8. Genetic gains (% of mean value) using different selection strategies. For DEC_h and DEC_w positive numbers are adverse (increased incidence) and negative number favourable (reduced incidence).

Index	D	BD	CEL	BR	DEC_h	DEC_w
1. Growth [i]	20	-4	3	3	-3	6
2. Wood chips [ii]	8	3	1	7	-3	10
3. Kraft pulp [iii]	13	1	2	6	-1	11
4. Growth + wound-rot resistance [iv]	19	-5	3	3	5	-11
5. Wood chips + wound-rot resistance [iv]	4	4	1	6	-5	-11
6. Kraft pulp + wound-rot resistance [iv]	11	2	2	7	4	-8
7. Heart-rot resistance [v]	4	-1	0	-1	-38	8
8. Wound-rot resistance [v]	5	-1	1	1	13	-46

[i] Selecting for D only.

[ii] Economic weights to maximise profit per ha from production of wood chips. Data and methods are from Borralho *et al.* (1993). Weights have been converted to standard deviation units and relative weights are 1 each for D and BD.

[iii] Economic weights to maximise profit per ha from production of unbleached kraft pulp. Weights are from Greaves *et al.* (1997a) and have been converted to standard deviation units. Relative weights are 1, 1 and 0.3 for D, BD and CEL respectively.

[iv] Same indices as 1, 2 and 3 with selection for DECw.

[v] Selecting for DEC_h or DEC_w only.

Gains were much less for multi-trait selection (Table 5.8). If wound-rot was included in a growth, wood chip or kraft pulp index then the predicted gains were approximately 10% which represents a shift in the incidence from 0.50 to 0.45. The pattern was similar for heart-rot (data is not shown), although gains were higher, and the shift in the incidence is predicted to be from 0.50 to 0.42.

5.4 DISCUSSION

5.4.1 Selecting for decay resistance

One of the key quality criteria when producing high value *E. nitens* veneer or appearance products is that the pruned wood be free of defects such as decay. Data from this study suggests tree breeding is a tool that can be used to manage decay. However, before any breeding plan for decay resistance can be implemented it is essential that the selection method be appropriate to meet the objective described above.

Finding a suitable selection trait

The objective of a breeding program for decay resistance is to select trees that can either resist decay establishing or can contain the spread of decay over the length of a rotation. Management practices in plantations grown for sawlog production provide opportunities for decay fungi to enter via pruning and thinning wounds. Therefore one objective is to select trees that can contain decay initiated by such wounding to the stem. Ideally, a tree breeder needs an assessment method that can be used at a reasonably young age, and in a manner that does not destroy the tree. However, finding a suitable selection trait for decay resistance is complex. This is because a range of tree responses influences the establishment and spread of decay in *E. nitens* and therefore observed decay may actually be a number of different traits. Furthermore, tree responses appear to differ between sites (Mohammed *et al.* 1999, Barry 2001) and these differences may lead to genotype by environment interactions in the direct measurement of decay incidence. In this study two types of decay were studied; heart-rot, which was an advanced stage of decay in the centre of the tree; and wound-rot, which was an early stage of decay arising from wounds to the sapwood. These represent the culmination of a range of the trees responses but they are not direct measures of the breeding objective trait, which is decay-free timber at harvest age. Therefore a key issue in determining the functionality of heart-rot and wound-rot measures is to consider how they might be related to the breeding objective trait.

Resistance to wound-rot would appear to be a good early measure of the breeding objective trait and consequently may be an important selection trait for sawlog plantations. Wound-rot, as assessed here, primarily measured the resistance to the longitudinal spread of decay from sapwood wounds. In genotypes with a low

incidence of wound-rot, the longitudinal spread of decay was significantly slower than in other genotypes. This probably indicates the xylem defence mechanisms described by Barry (2001) are well developed in these genotypes. However, such differences are only economically important if they indicate a tree's ability to contain the establishment and spread of decay in the long term. This question can only be answered by doing long-term studies.

The suitability of heart-rot as a selection trait for the breeding objective (that is decay free timber at harvest age) appears less clear. Heart-rot represents a more advanced stage of decay arising from damage to the tree, although in this case the damage was due to chance natural means and not deliberate wounding. Decay from sapwood wounds can develop in the heartwood directly through pruned or naturally shed branches (Barry *et al.* 2000), from centripetal spread via the relatively weak barrier of wall 2 (Shigo and Marks 1977) or simply from the natural transition of sapwood into heartwood (Chattaway 1952). Wound-rot and heart-rot may therefore represent different stages in a continual process. However, in this study heart-rot and wound-rot were genetically unrelated (see Table 5.6) and therefore appear to be different traits. There are two possible reasons for these differences. Firstly, it might reflect the different entry points for decay fungi (controlled wounding compared to natural damage) and therefore reflect different environments for the initial establishment of decay fungi. Secondly, it may reflect different host mechanisms involved in containing decay in the heartwood and sapwood. If the first scenario were true, it would mean that the measure of heart-rot is a measure of the naturally occurring decay and may have application if these levels are high. However, studies of decay in *E. nitens* have shown that heart-rot developing through naturally shed branches has a lower incidence than decay developing through wounds (Wardlaw and Neilsen 1999, Mohammed *et al.* 2000). Also, it remains to be seen to what extent naturally occurring heart-rot is contained within the knotty core at harvest age. If it is contained, then heart-rot is probably not an important trait for breeding programs. If the latter scenario were true, then measuring the early stages of wound-rot would have a poor correlation with the breeding objective and other selection traits may be required to get good gains in the objective trait.

Another important issue regarding the applicability of selection methods for decay is to ensure they are not strongly influenced by genotype by environment interactions, that is, to ensure is the traits are stable across different sites. As stated above, studies of the fundamental nature of defence mechanisms in *E. nitens* have suggested they may be different across sites (Barry 2001). Of the three sites studied, one site (Gog) had no evidence of heart rot in the core samples. This may be due to strong host defence mechanisms on that site, low-risk infection courts (e.g. small branches) or an unfavourable environment for infection by decay fungi. For the other two sites, heart rot was detected and

although the incidence varied, the correlation of family means was fairly high (0.77) but less than unity, indicating a degree of genotype by environment interaction. Many factors may have contributed to this apparent interaction, including all aspects of the tree's defence response, differences in the range of decay fungi present, and differences in the infection courts that from which decay developed. However, in terms of breeding strategy, the reasonably high correlation of family means is encouraging and suggests that, where heart rot is present, it should be consistent in terms of family effects, across sites. Wound-rot was only assessed on one site and no conclusions can be drawn about genotype by environment interactions. Obtaining wound-rot assessments across multiple sites is therefore a priority to evaluate the robustness of direct measurements.

Assessment methods

The method used to measure the incidence of wound decay appears to be an effective way of selecting for decay resistance, although the method needs further testing to ensure it works consistently. The method worked, by chance, on one site (Gog) but not on the other two sites because the incidence was too low to detect genetic differences. The method simply measured the incidence of decay fungi establishing in the wound and travelling more than 10 cm longitudinally in the sapwood after a fixed time interval (10, 12 and 16 months at Dial, Gog and Kamona respectively). What is being measured is the ability of the tree to contain decay after an entry point has been provided. With some basic studies to define distances and time intervals it should be possible to reliably use this method over different sites.

An important issue regarding this methodology is to make sure differences in wound-rot resistance are well related to the containment of decay until harvest age. This study has shown that, for some genotypes, the spread of decay is significantly slower than for others. However, these differences are only economically important if they indicate a tree's ability to contain the spread of decay in the long term. Or to express this in another way; data is needed to show that the selection trait, that is the containment of decay after about 12 months, is well related to the objective trait, which is decay free timber at rotation age. This question can only be answered by doing long term studies.

Some other selection methods

Severity of decay was also evaluated as a selection trait but was found to be unreliable. Severity was measured as the percentage of the core length that was decayed. For heart-rot data, values ranged from 0 to 28% with a mean of 3% and analyses were done on arcsine-square-root transformed data due to non-normality. Heritabilities and genetic correlations were significant but were found to be strongly dependent on a small number of severely affected trees and, by excluding

these trees, very different values could be obtained. It appears that when severity is low then incidence data is the most reliable way of evaluating decay. Similar results were found when studying butt rot in *E. obliqua* (Wardlaw 2002) where it was concluded severity data gave strongly biased results when severity was low.

The incidence of discolouration was evaluated as a decay selection trait but was found to be ineffective. A brown discolouration occurs at the interface of decay infection where phenols are deposited (Barry 2001) and it was thought that this discolouration may provide an early warning to decay and improve the capacity to detect the onset of decay. However, the presence of discolouration was difficult to determine on cores and therefore appears to be an imprecise method of detecting decay. Although incidence of decay and discolouration were well correlated ($r_g = 0.80$ and 0.71 for heart-rot and wound-rot respectively), heritabilities for discolouration were much lower and had very high standard errors ($h^2 = 0.14 \pm 0.13$ and 0.20 ± 0.24 for heart-rot and wound-rot respectively).

Another selection trait evaluated as an indirect measure of decay was extractives content. Extractives have been shown to accumulate in response to decay in *E. nitens*, and methanol extracts were found to be six times greater in the reaction zone compared to healthy sapwood (Barry *et al.* 2000). However, in the current study there were no relationships between extractives content and the incidence of heart-rot or wound-rot. Furthermore, there were strong genotype by site interactions for extractives content indicating that the processes that cause the production of extractives are very site specific. Therefore it appears that the extractives content of core samples cannot be used as an indicator of a trees response to decay and, due to the high genotype by site interactions, are unlikely to be able to be used as a trait in breeding programs.

5.4.2 Applying appropriate economic weights

Substantial gains in either heart-rot or wound-rot resistance were only obtained when selecting for that trait alone. Selecting for either wound-rot or heart-rot in isolation may be an option if a deployment population was required for a site known to be decay prone. If the incidence of decay was at a level that made the wood valueless for the intended market, then this may be an economically advantageous option for the forest manger. This situation may arise on highly productive sites in moist environments, which have been shown to have a high probability of decay developing from pruning wounds (Mohammed *et al.* 2000).

However, under most circumstances selecting for decay resistance would be a part of multi-trait selection. Table 5.8 suggests that gains in wound-rot and heart-rot resistance in multi-trait selections (approximately 5-10% reduction) are unlikely to be of any practical consequence if seeking to limit decay. Nevertheless, selecting in this way may be appropriate for a breeding population where the aim

was to ensure the selected population became 'no worse' for decay incidence. There is a tendency for wound-rot to worsen when selecting for other traits (see indices 1, 2 and 3 in Table 5.8) but it appears this can be avoided with very little loss in stem volume, basic density or cellulose content by also selecting for decay resistance (compare indices 4, 5 and 6 in Table 5.8).

5.4.3 Importance of branching for decay

There is a strong linear relationship between branch size and the proportion of decay escapes (Wardlaw and Neilsen 1999) and, using the relationship of Wardlaw and Neilsen, it can be shown that a 10 mm increase in branch size is predicted to cause a 13% increase in decay escapes. Therefore breeding to reduce branch size may be an effective strategy to minimise the risk of decay.

However, branching is under weak genetic control (Table 5.5) and only small changes in branch size can be made through tree breeding. Therefore selecting to reduce branch size will do little to change the risk of decay. At best, if selecting for branching alone, the reduction in branch size is estimated to be 6%. In a typical *E. nitens* plantation this would reduce branch size by about 4 mm, which would result in a reduction in the proportion of decay escapes by only 5%. However, selecting for branching alone is not something that would be normally done – branching would always be a component in multi-trait selection. In a multi-trait index of diameter and branching (with, say, equal emphasis on each trait) the reduction in branch size would be about 4%, the change in branch size about 2 mm, and the reduction in decay escapes only 2.5%. Changes of this size would have little practical impact on problem sites where the decay incidence can be as high as 76% (Mohammed *et al.* 2000).

5.5 CONCLUSION

The incidences of wound-rot and of heart-rot appear to be under strong genetic control. Both traits can be assessed easily using cores although more work in needed to precisely define the method for assessing wound-rot. Data was found to be most reliable when assessed as a binary variable. Long term studies are also needed to ensure the assessment method used in this study is a reliable indicator of the containment of decay at harvest age. Assessments of the severity of decay were not reliable, probably due to the low incidence and non-normality of the data. Decay could not be reliably assessed using the presence of discolouration and quantities of ethanol soluble extractives.

Wound-rot will probably be the trait that will be most relevant to improving the value of *E. nitens* sawlog plantations. However, for multi-trait selection, large gains in this trait do not appear possible and an appropriate selection strategy may be to ensure the incidence of decay becomes no worse than it is in the current

population. This appears achievable without sacrificing large gains in other traits. Good gains appear possible when selecting for decay resistance alone though gains in other traits are forgone. This strategy may be appropriate if selecting a deployment population for problem sites. Problem sites appear to exist but data is needed to determine the degree to which trees contain decay at harvest age.

CHAPTER 6

6. Breeding for Improved Wood Stiffness

6.1 INTRODUCTION

Stiffness and strength are of critical importance for structural timber (SA 1997). Stiffness defines the bending strength under load and is a term used to describe the elastic properties of wood (Ilic 2001). It is generally measured using static bending tests and expressed as the modulus of elasticity (MOE). Stiffness is an important property for structural timber because a lack of stiffness manifests as sagging roof lines or bouncing floors. Strength, which is generally considered less important than stiffness, defines the maximum load capacity and is measured as the modulus of rupture (MOR). Stiffness and strength are used to define structural timber grades. For example, Australian Standard (AS) 1720.1 uses MOE and MOR to classify sawn timber into 10 stress grades (called F grades) for use as structural products (SA 1997), and AS 2878 classifies timber species into strength groups based on typical values for MOE and MOR (SA 2000).

The stiffness of timber is closely related to wood density and microfibril angle (MFA). In both hardwoods and softwoods stiffness, has been observed to have a strong negative correlation with MFA and a positive correlation with density (Cave and Walker 1994, Evans and Ilic 2001). These studies have found MFA to be the major determinant of wood stiffness. Stiffness is also related to knot size (e.g. Yang and Waugh 1996a) although this appears to have a smaller effect and is strongly influenced by forest management practices. MFA, which is the angle of the cellulose microfibrils in the secondary cell wall (Downes *et al.* 1997), is also thought to influence the dimensional stability of timber (Donaldson and Turner 2001). Therefore it is a property of wood that is of increasing interest. For *E. nitens*, within and between tree variation in MFA has been extensively studied by Evans *et al.* (2000).

The stiffness of eucalyptus species harvested from native forests, including *E. nitens*, have been well documented (e.g. Hillis 1978, SA 2000). However, it is recognised that stiffness data from native forest timber, which is generally harvested at ages of greater than 80 years, will not be transferable to plantation timber which is expected to be harvested at between 20 to 30 years (Hillis 1978, Yang and Waugh 1996a, Ashley and Ozarska 2000). Studies for plantation grown *E. nitens* have been done by McKimm (1985), Waugh and Yang (1996b) and

McKenzie and Gaunt (2001). All studies found plantation grown *E. nitens* to have much lower strength properties than native forest *E. nitens* and differences were attributed to age affects. The study by McKimm (1985), using 8.5 year old timber, found that strength was comparable to *Pinus radiata*, and the studies by Yang and Waugh (1996b) and McKenzie and Gaunt (2001), using 15 to 29 year old timber, found average strength to be significantly greater than that of *P. radiata*. Studies on the strength of other plantation grown eucalypts have been reported by Yang and Waugh (1996a, b), Ashely and Ozarska (2000) and Dickson *et al.* (2003). These studies concluded that plantation eucalypts generally have high strength properties although they are less than those for native forest timber. All studies have found plantation timber to have high variation in stiffness.

The genetic control of wood density in *E. nitens* and other eucalypt species has been well studied (e.g. Muneri and Raymond 2000, Chapter 3 of this thesis). However, there have been no published studies of the genetic control of stiffness or MFA in *E. nitens* or, it appears, in any other eucalypt species. The aims of this study were to investigate the genetic control of stiffness in *E. nitens*, to estimate the genetic gains that can potentially be made in stiffness using different selection strategies, and to explore options for the genetic improvement in stiffness in breeding programs. In addition to this, genetic parameters for MFA are reported.

6.2 MATERIALS AND METHODS

6.2.1 Trial establishment

The genetic material was open-pollinated progeny of 34 native forest families from the Toorongo Plateau in the central highlands of Victoria. Mother trees were growing as a pure stand in an open forest and stem diameters ranged from 35 to 110 cm. The location is described in Pederick (1979).

The progeny trial was established in 1984 at Kamona in north-eastern Tasmania (latitude 41° 08'S: longitude 147° 40'E). This trial was part of a series of three trials, although data from only one site is reported here. The rainfall and altitude of this site is, respectively, 1150 mm and 160 m. This is a productive site, with a site index of 28.6 m (the mean dominant height at 15 years) and a total volume of 268 m^3 ha^{-1} at 12 years. Stocking at planting was 1111 trees ha^{-1} (3 m by 3 m spacing) and survival at age 12 years was 66%. The trial design was a randomised complete block with single tree plots and 16 replications per site.

6.2.2 Trial assessment

A total of six traits were assessed for this study and Table 6.1 summarises the data for each trait. All trees were measured for diameter at breast height (1.3 m) at 12 years. Trees less than 10 cm diameter were excluded from diameter and wood

property assessments. Trees of this size were all strongly suppressed with no diameter increment between ages 6 and 12, and had atypical wood properties. These trees were found to inflate error variances.

Basic density was measured at 12 years and was assessed using a single 12 mm diameter bark to bark core at a height of 0.9 m. Core sampling at this height has been shown to be a reliable predictor of whole tree values of basic density (Raymond and Muneri 2001, Chapter 2 of this thesis). Basic density was defined as oven-dry wood mass per unit volume of green wood, and was measured using the water displacement method (Hendrichs and Larson 1970; TAPPI 1989). An average of 8 trees per family were randomly sampled.

Table 6.1. Description of data.

Trait		unit	age	mean	min.	max.	sd [i]	n [i]
DBH	Diameter over bark at 1.3 m	cm	12	22.7	10.2	40.4	6.6	354
BD_{core}	Basic density of core	kg m^{-3}	12	449	375	539	29	244
CEL	Cellulose content	% kg kg^{-1}	13	41.6	38.5	44.4	1.3	187
AD_{silvi}	Air dried density (Silviscan) [ii]	kg m^{-3}	10	567	465	731	46	169
MFA	Microfibril angle (Silviscan) [ii]	degrees	10	14.7	11.9	19.2	1.4	169
MOE	Modulus of elasticity (Silviscan) [ii]	GPa	10	11.0	7.8	16.8	1.5	169

i) sd is the phenotypic standard deviation and n is the number of samples.

ii) For AD_{silvi}, MFA and MOE measurements were made for each growth ring between ages 2 and 10 years. The data shown are individual tree averages combined across growth rings.

Crude cellulose content (g cellulose per wood dry mass) was assessed at 13 years using 12 mm bark to bark core samples taken at a height of 0.9 m. Core sampling at this height is a reliable predictor of whole tree values of cellulose content (Chapter 2 of this thesis). Wood cores were dried at 27°C, ground and assayed using the method of Wallis *et al.* (1997). This method involves digesting in diglyme and hydrochloric acid to dissolve non-cellulosic compounds and then collecting the cellulose residue by filtration. Five trees were randomly sampled per family. More details of the sampling and analysis are given in section 3.2.1.

Densitometry measurements were made using Silviscan-2, which measures a density profile at 50μm intervals using x-ray techniques. Details about Silviscan-2 are given in Evans *et al.* (2000) and Evans and Ilic (2001). In this study, five trees were sampled per family with measurements being made on a bark to pith strip taken (by coring) from a height of 0.9 m. Following x-ray scanning, growth ring boundaries were manually inserted the density profiles and average densities for each growth ring calculated. Density profile data were normalised using measurements of mass and volume made on the test samples (which were typically 2 mm by 7 mm by 120 mm). These measurements were made after drying and at a room moisture content and are therefore assumed to be air-dried densities (as distinct from basic densities).

Microfibril angle (MFA) was also estimated using Silviscan-2. Sample strips were the same as those used for densitometry and, as for density, data was separated by growth rings and average MFA's were calculated for each growth ring. Measurements of MFA taken near breast height have been found to be good predictors of whole tree values (Evans *et al.* 2000).

Stiffness was measured as the modulus of elasticity (MOE), and was calculated using the empirical relationship between density (D) and MFA which is:

$$MOE = 0.284\ D / MFA \quad \textbf{(6.1)}$$

This relationship was defined by Evans and Ilic (2001) and has been found to be appropriate across a wide range of species. It was used to estimate MOE for each individual growth ring.

6.2.3 Estimation of genetic parameters

All traits were analysed in a multivariate analysis using ASREML (Gilmour *et al.* 1999). The model estimated variances, covariances, correlations and errors for each trait simultaneously. Multivariate analyses use information more efficiently and can improve the precision of genetic parameters when selected subsets of data are used (Dieters *et al.* 1999). The model was:

$$Y = \mu + REP + FAM + \varepsilon \quad \textbf{(6.2)}$$

where Y is a vector of data for each trait; μ is the mean for each trait; REP are replicate effects fitted as a fixed factor; FAM are family effects fitted as a random factor; and ε is a vector of residuals for each trait. The model terms FAM and ε included an inter-trait variance and covariance matrix pooled across sites.

Heritabilities and their standard errors were calculated by ASREML as:

$$h^2 = \sigma^2_f / r\,(\sigma^2_f + \sigma^2_e) \quad \textbf{(6.3)}$$

Where h^2 is the narrow sense heritability; σ^2_f and σ^2_e are, respectively, the variance components for FAM and ε estimated in model 6.2; and r is the coefficient of relationship. The coefficient of relationship used was 0.4 which assumes a selfing rate of approximately 30% (Griffin and Cotterill 1988). However, more recent studies have suggested that a 30% selfing rate may be at the upper end of measured values for *E. nitens* (Grosser *et al.* 2001) and therefore there is a risk that heritabilities may be slightly inflated.[xi]

6.2.4 Estimation of genetic gains

Genetic gains for diameter, basic density, cellulose content, and stiffness were estimated under five selection strategies. This was done by calculating individual

[xi] See section 3.2.2 for more details.

tree breeding values for each trait and then using these breeding values to estimate gains in selected populations under each selection strategy. For each selection strategy, the assortment of structural grade boards was estimated using breeding values for stiffness.

Individual tree breeding values were calculated using ASREML to fit the following multivariate model:

$$Y = \mu + REP + TREE + \varepsilon \quad (6.4)$$

Where Y, μ, REP and ε are as previously defined and TREE are individual tree breeding values (additive genetic) for diameter, basic density, cellulose and stiffness (MOE). The terms TREE and ε included inter-trait variance and covariance matrices. Correlations were fixed to values calculated in model 6.2 and a coefficient of relationship of 0.4 was assumed for calculating additive genetic variances.

Five selection strategies were evaluated with each strategy applying different sets of economic weights to traits (Table 6.2). The weights describe the relative importance of a standard deviation unit of that trait. The growth index (1) maximises volume per hectare. The wood chip index (2) maximises profit per hectare from wood chip production. Index values were based on those of Borralho *et al.* (1993) with weights converted to standard deviation units. The kraft pulp index (3) maximises profit per hectare for unbleached kraft pulp production. Index values are taken from Greaves *et al.* (1997a) and have also been converted to units of standard deviation. The stiffness index (4) maximises stiffness, or maximises recovery of high strength timber. The structural sawlog index (5) is intended to represent an index that maximises profit per ha when selling structural grade products and places weights on volume and high stiffness. These weights are not true economic weights because no economic information has been used – they are estimates used here to demonstrate the effect of using stiffness as part of multitrait selection.

Table 6.2. Economic weights (in standard deviation units) for selection indices.

Index	D	BD	CEL	MOE
1. Growth	1	0	0	0
2. Wood chip	1	1	0	0
3. Kraft pulp	3	3	1	0
4. Stiffness	0	0	0	1
5. Structural sawlog	3	0	0	2

For each selection strategy individual tree index values were calculated as:

$$I = BV_D.W_D/\sigma_D + BV_{BD}.W_{BD}/\sigma_{BD} + BV_{CEL}.W_{CEL}/\sigma_{CEL} + BV_{MOE}.W_{MOE}/\sigma_{MOE} \quad (6.5)$$

Where I is a unitless index value, BV is the breeding value for each trait (see Table 6.1 for definition of subscripts), σ is the additive genetic standard deviation for these traits; and W is the economic weight for each trait. The economic weights used for each index are shown in Table 6.2.

The top 20 trees were selected for each selection strategy and then average breeding values for diameter, basic density, cellulose, and MOE calculated. These were then expressed as a percentage change from the unselected population. The selected population consisted of 20 trees from a population of 354, or 5%.

The assortment of structural grade boards was estimated for each selection strategy. This was done by converting the selection trait (which was Silviscan MOE) to the breeding objective trait (which was average MOE at harvest age) and using this value to predict the mix of board grades. This assumes that Silviscan predicted MOE is the primary determinant of structural board grades. A genetic correlation of $r_G = 0.8$ was used to convert Silviscan MOE to MOE at harvest age. Structural board grades were defined according to the groupings used in SA (1997) and SA (2000), which are official standards used to classify timber into strength groups. These groups and the thresholds used to classify them are shown in Table 6.8. The proportions of boards in each of these grades were estimated using the cumulative probabilities of the standard normal distribution. A standard deviation of 3.8 GPa was assumed which is the standard deviation calculated when treating each individual ring on each tree between ages 3 and 10 years as a separate measure. This standard deviation was used, rather than a single tree average (see Table 6.1), to account for some of the within tree variation in MOE.

6.3 RESULTS

6.3.1 Age differences

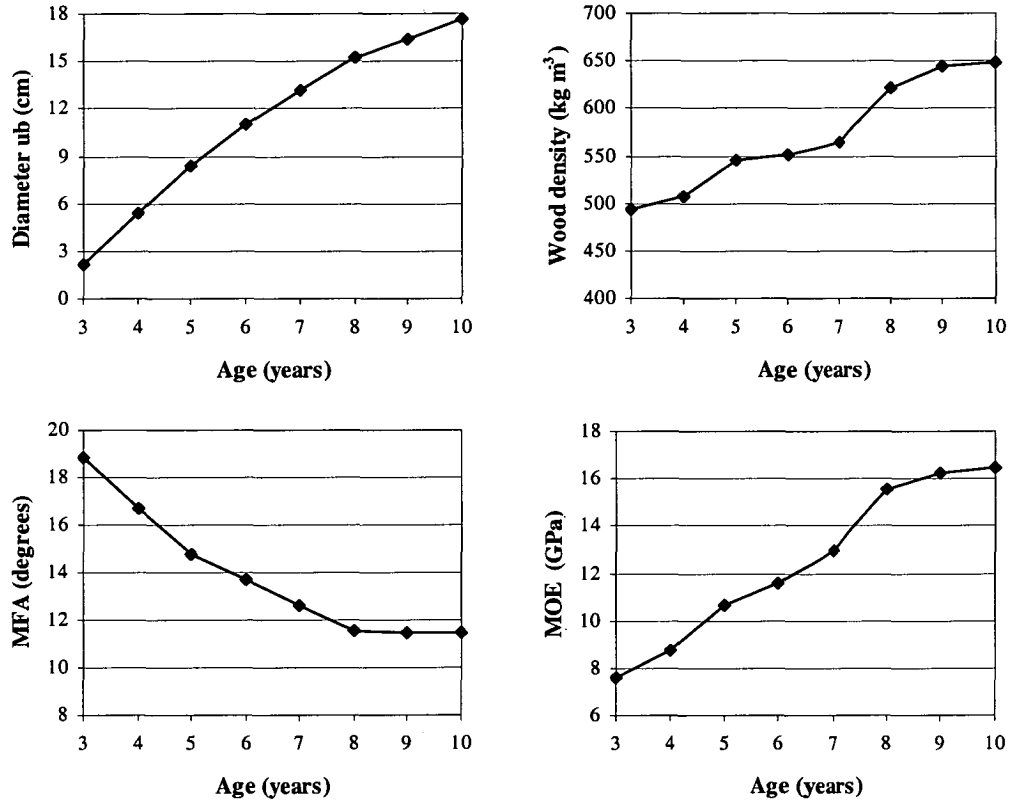
There were large and statistically significant age differences for wood density, MFA and MOE (Figure 6.1). Air-dried wood density increased with age. The average density of wood layed down at 3 years was 500 kg m^{-3} and at age 10 years this had increased to 650 kg m^{-3}. There were large differences between trees at all ages. At age 3 years the values ranged from 389 to 616 kg m^{-3} and at 10 years the range was 499 to 877 kg m^{-3}.

MFA decreased with age, with average values ranging from 19 degrees at age 3 years to 12 degrees at 10 years. There were also large differences between trees at all ages. At age 3 years, values ranged from 13 and 28 degrees and at 10 years the range was 8 to 19 degrees.

The predicted MOE, which was calculated from density and MFA, increased sharply with age. Values doubled between ages 3 and 10 years, with an average

of 8 GPa for wood layed down at 3 years and 16 GPa for 10 year old wood. These trends and the range of values for density and MFA are very similar to those reported by Evans *et al.* (2000) in another study on *E. nitens*.

Figure 6.1. Variation with age for diameter under bark, air dried wood density, microfibril angle (MFA) and modulus of elasticity (MOE). All measurements were made using Silviscan-2 on wood cores taken at a height of 0.9 m.



6.3.2 Heritabilities

The heritability for density measured using Silviscan was slightly higher than that measured directly from wood cores (0.67 compared with 0.54) although differences were not statistically significant (Table 6.3). Heritabilities of density varied between growth rings (Table 6.4) and were highest in rings layed down at age 6 years and significantly lower for both younger and older wood. This was a similar pattern to that reported by Greaves *et al.* (1997b), also for *E. nitens*, although the absolute values for heritabilities were higher in this study.

The heritability for MFA averaged across all growth rings was 0.38 (Table 6.3), indicating this is a trait under moderate genetic control, and values were not significantly different between growth rings (Table 6.4). MOE had a heritability of 0.56 when averaged across all growth rings (Table 6.3) and there were some

differences in different growth rings. Heritability was significantly lower in wood layed down at four years, but did not appear to vary between 6 and 10 years.

Table 6.3. Heritabilities and variance components (± standard errors) measured across all growth rings.

Trait	Unit	h^2	σ^2 family	σ^2 error
DBH	cm	0.30 ± 0.12	5.3 ± 2.3	38.8 ± 3.1
BD_{core}	kg m^{-3}	0.54 ± 0.17	182 ± 66	657 ± 69
CEL	% kg kg^{-1}	0.72 ± 0.21	0.50 ± 0.18	1.22 ± 0.15
AD_{silvi}	kg m^{-3}	0.67 ± 0.21	662 ± 260	1829 ± 232
MFA	degrees	0.38 ± 0.19	0.28 ± 0.16	1.74 ± 0.22
MOE	GPa	0.56 ± 0.20	0.89 ± 0.38	3.10 ± 0.39

Table 6.4. Changes in heritabilities (± standard error) with age for diameter under bark (D_{silvi}), air dried density (AD_{silvi}), microfibril angle (MFA) and modulus of elasticity (MOE).

Age	D_{silvi} [i]	AD_{silvi} [ii]	MFA [ii]	MOE [ii]
4	0.31 ± 0.19	0.38 ± 0.19	0.36 ± 0.19	0.40 ± 0.19
6	0.38 ± 0.19	0.75 ± 0.22	0.42 ± 0.19	0.68 ± 0.21
8	0.43 ± 0.20	0.51 ± 0.21	0.36 ± 0.18	0.54 ± 0.21
10	0.43 ± 0.20	0.35 ± 0.20	0.54 ± 0.18	0.64 ± 0.21

i) D_{silvi} values are total cumulative under bark diameter at each given age.

ii) AD_{silvi}, MFA and MOE were calculated using the individual growth ring corresponding to that age only.

6.3.3 Correlations

Favourable genetic and phenotypic correlations occurred between density and MFA and between cellulose and MFA (low MFA is favourable) although the genetic correlations had high standard errors (Table 6.5). There was an adverse genetic correlation between diameter and MFA but this also had a high standard error. As reported in other studies on this trial (Chapter 3 of this thesis), there was an adverse correlation between diameter and density, and a favourable correlation between diameter and cellulose. There were strong phenotypic and genetic correlations between MOE and density, and between MOE and MFA (Table 6.5). However, since MOE was derived from these traits, this is as expected.

The phenotypic and genetic correlations between basic density measured on a wood core and air dried density measured using Silviscan were high with values of $r = 0.77$ and $r_G = 0.98 \pm 0.05$ respectively. Therefore these can be considered different assessments of the same trait. Correlations between basic density-MFA and basic density-MOE are not shown, but were almost identical to those between AD_{silvi} -MFA and AD_{silvi} -MOE (see Table 6.5).

Table 6.5. Genetic correlations (r_G) above diagonal (± standard errors) and phenotypic correlations (r) below diagonal.

	D	AD_{silvi}	CEL	MOE	MFA
D		-0.67 ± 0.22	0.72 ± 0.18	-0.60 ± 0.24	0.20 ± 0.33
AD_{silvi}	-0.08		-0.14 ± 0.27	0.85 ± 0.09	-0.34 ± 0.28
CEL	0.40 **	0.13 *		0.09 ± 0.28	-0.48 ± 0.25
MOE	-0.13 *	0.78 **	0.34 **		-0.78 ± 0.13
MFA	0.10	-0.30 *	-0.40 **	-0.80 **	

** = significantly different from zero at P<0.01

* = significantly different from zero at P<0.05

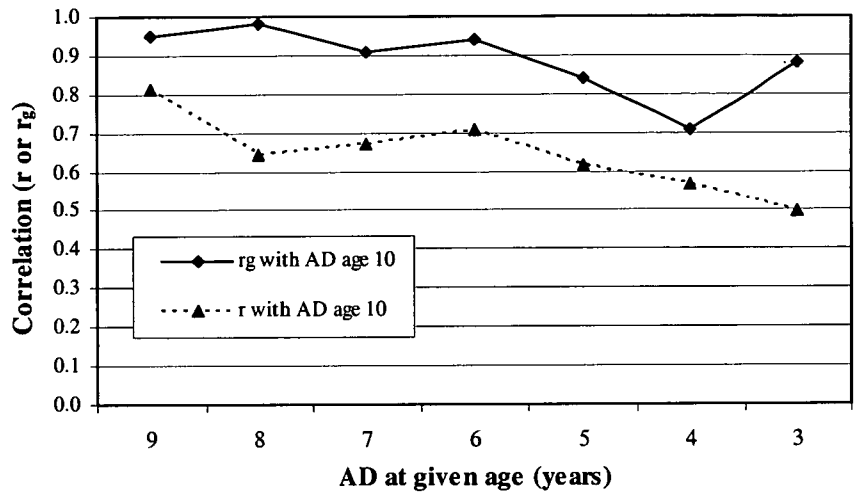
Age-age correlations were determined for wood density, MFA and MOE. There was a trend for correlations to decrease as age differences increased. These trends are illustrated in Figure 6.2, in which the genetic and phenotypic correlations between the age 10 growth rings are compared to all other ages. For wood density, correlations between ages were generally strong and it appears that the same genes control wood density at different ages. This is a very similar pattern to that measured by Greaves *et al.* (1997b). However, for MFA a different pattern was observed. Correlations decreased steadily as age differences increased to the point where MFA at age 3 to 4 years appeared to be unrelated to MFA at age 8 to 10 years (Figure 6.2). This suggests that there are different genes controlling MFA at different ages. For MOE, correlations between ages decreased gradually as age differences increased. Genetic correlations were mostly reasonably strong, and were never less than $r_G = 0.5$.

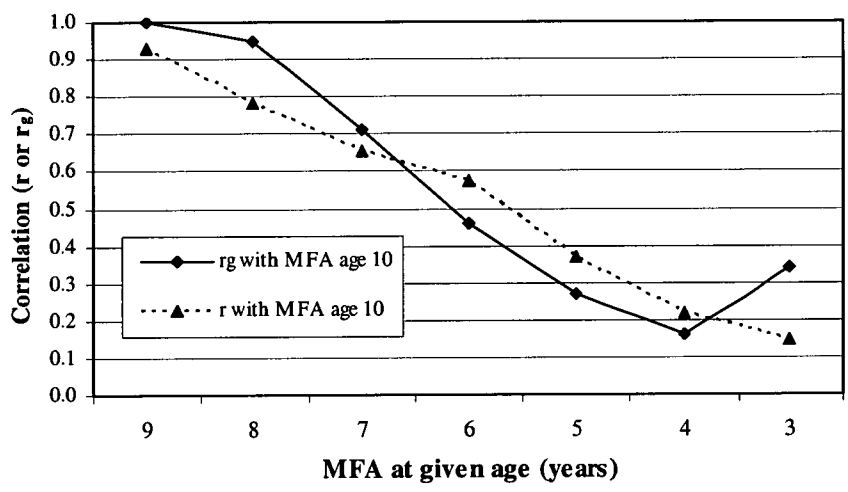
Correlations between the average values (across all growth rings) and individual growth rings for wood density, MFA and MOE are shown in Table 6.6. For all traits the average tree value was a reasonable predictor of any individual growth ring. Genetic correlations were always greater than $r_G = 0.8$, despite tendencies for low correlations between some individual pairs of growth rings (Figure 6.2). Therefore, if selecting for density, MFA, or MOE, there appears no need to base selection on a particular growth ring, or group of growth rings. This means the time consuming step of separating measurements by growth rings can be avoided.

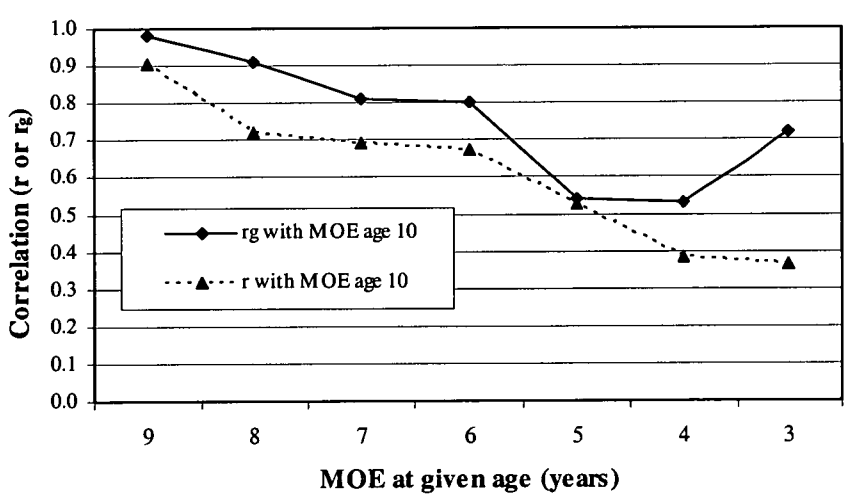
Table 6.6. Genetic correlations (r_G) with standard errors and phenotypic correlations (r) for air dried density (AD_{silvi}), microfibril angle (MFA) and modulus of elasticity (MOE) between average values (across all growth rings) and individual growth rings.

Age	ADsilvi		MFA		MOE	
	r_G	r	r_G	r	r_G	r
4	0.95 ± 0.05	0.84	0.82 ± 0.10	0.79	0.86 ± 0.07	0.70
6	0.99 ± 0.02	0.93	0.98 ± 0.05	0.89	0.98 ± 0.03	0.90
8	1.00 ± 0.04	0.87	0.91 ± 0.08	0.85	1.02 ± 0.03	0.92
10	0.96 ± 0.10	0.82	0.83 ± 0.11	0.69	0.90 ± 0.06	0.85

Figure 6.2. Age:age genetic (rG) and phenotypic correlations (r) for air dried wood density (AD), microfibril angle (MFA) and modulus of elasticity (MOE). Graphs show correlations between age 10 value and values at ages 9 to 3 years.







Correlations between MOE-AD_{silvi} and MOE-MFA for individual growth rings are shown in Table 6.7. Genetic correlations between MOE-AD_{silvi} increase for older wood. This may be due to a greater influence of MFA in determining the stiffness of juvenile wood. Genetic correlations between MOE-MFA are were significantly different across individual growth rings.

Table 6.7. Genetic correlations (r_G), with standard errors, and phenotypic correlations (r) between modulus of elasticity (MOE) and air dried density (AD_{silvi}), and between MOE and microfibril angle (MFA) for individual growth rings.

Age	MOE and AD_{silvi}		MOE and MFA	
	r_G	r	r_G	r
4	0.74 ± 0.15	0.73	−0.82 ± 0.11	−0.83
6	0.86 ± 0.08	0.78	−0.76 ± 0.14	−0.82
8	0.94 ± 0.06	0.85	−0.73 ± 0.19	−0.82
10	0.96 ± 0.09	0.75	−0.79 ± 0.19	−0.81

6.3.4 Genetic gains

The predicted gains in MOE and the distribution of structural timber grades under different selection strategies are shown in Table 6.8. Selecting for stiffness alone is predicted to cause a 16% increase in MOE and significant increases in the proportions of boards meeting high structural grades. However, this selection strategy will also result in a 20% decrease in diameter. When selecting on the wood chip, kraft pulp, or (hypothesised) structural sawlog index predicted gains in MOE are, respectively, 8%, 5% and 11%. Despite these different gains in MOE, the proportions of boards in each structural grade are very similar and therefore there will probably be no practical differences between these strategies in terms of the value of structural products. Selecting for diameter alone will cause a 7% decrease in MOE and a decrease in the proportion of timber meeting high structural grades.

Selecting for stiffness using average, juvenile and mature wood stiffness gave very similar results. The genetic gains shown in Table 6.8 for indices 4 and 5 were based on selecting for MOE averaged across all growth rings. Data on gains in each trait and the distribution of structural timber grades when selecting using juvenile and mature MOE are not included here, but were almost identical to those for average tree MOE.

Table 6.8. Genetic gains (% of mean value) and distribution of structural timber grades using different selection strategies. Structural timber grades are defined by MOE (GPa) and grade definitions are based on AS 1720.1 (SA 1997).

Index	Genetic gains (%)				Structural grades (%)					MOE
	D	BD	CEL	MOE	<6.9 Utility	6.9-9.1 F5	9.1-12 F8	12-16 F14	>16 F22	(GPa)
Current population	0	0	0	0	8	19	29	32	11	11.4
1. Growth [i]	23	-4	3	-7	12	23	30	28	8	10.6
2. Wood chip [ii]	7	3	3	8	5	15	27	36	16	12.2
3. Kraft pulp [iii]	12	1	4	5	6	16	28	35	14	12.0
4. Stiffness [iv]	-20	8	-1	16	3	11	24	39	23	13.2
5. Struct. sawlog [v]	3	3	3	11	4	14	26	38	18	12.6

i) Selecting for D only.

ii) Economic weights to maximise profit per ha from production of wood chips. Data and methods are from Borralho *et al.* (1993). Weights were converted to standard deviation units and relative weights were 1 each for D and BD.

iii) Economic weights to maximise profit per ha from production of unbleached kraft pulp. Weights are taken from Greaves *et al.* (1997a) and have been converted to standard deviation units. Relative weights are 3, 3 and 1 for D, BD and CEL respectively.

iv) Selecting for stiffness only to maximise the recovery of high strength products.

v) Hypothesised economic weights to maximise value for a forest grower selling sawlogs for structural products. Relative weights, in standard deviation units, are 2 for D and 3 for MOE.

6.4 DISCUSSION

6.4.1 Importance of improved stiffness

The stiffness of wood is a fundamental measure of its quality and its ability to meet market requirements. Stiffness is the main quality criteria for structural properties (SA 1997) and is also important for high value appearance products such as furniture, flooring and architectural products (Ozarska 2000). Therefore consideration of the potential gains in stiffness under different selection strategies will always be necessary for breeding programs focusing on solid wood products. Different markets have different product requirements and the value of genetic gains in stiffness will be dependent on the market into which products are sold.

One possible market for hardwood structural products is general purpose framing products. This market is generally supplied by softwood timber and, to compete against a typical softwood (say *Pinus radiata*), the average MOE would need to be 10.5 GPa and the majority of output would need to be greater than 6.9 GPa (SA 2000). *E. nitens* appears to currently meet these specifications (Table 6.8, Yang and Waugh 1996b) and, for this market, strong emphasis on breeding for stiffness may not be required. However, some selection would be required because with no selection for stiffness (or wood density) a decline in stiffness is predicted due to an adverse correlation with growth.

Another, and probably more appropriate, market for hardwood structural products is high strength products. This market is generally supplied by native forest hardwood timber and, to compete in this market, the minimum MOE would need to be between 12.5 and 14 GPa (Hillis 1978, SA 2000). There would need to be an emphasis on selecting for stiffness if plantation grown *E. nitens* were to meet this threshold and be competitive in this market. After selection, it appears that this target can be achieved (Table 6.8). However, a proportion of boards will have stiffness values below this threshold (Table 6.8) and consequently higher value would be achieved from either additional gains, or by reducing the variability in stiffness.

Improved stiffness is also important for high value appearance grade products. Wood used in furniture and engineered products is required to have high strength and Ozarska (2000) nominates a threshold value of 12 GPa as being desirable for these products. This suggests selection for stiffness will also be important to meet the product specifications for appearance products, although these targets will probably be met when selecting to improve wood density or to decrease collapse (see Chapters 3 and 4).

6.4.2 Selecting for stiffness

Operational breeding programs selecting for stiffness need to consider the best and most cost effective way to select for this trait. This study suggests selecting for density alone can deliver a major proportion of potential genetic gains (compare selection indices 2 and 5 on Table 6.8). In addition, measuring density is at least 5 times cheaper than measuring stiffness and, for the same sampling budget, far more trees could be assessed for density than for stiffness. Therefore by using a cheaper sampling option it would be possible to screen a larger number of trees, increase the intensity of selection, and probably deliver greater genetic gains.

Other studies have found MFA to be the major determinant of stiffness due to a high phenotypic variation in this trait. For example, in *Pinus radiata* phenotypic values of MFA ranged from 10 to 40 degrees (Cave and Walker 1994) and in *E. nitens* the range was from 8.5 to 20 degrees (Evans and Ilic 2001). Therefore it may be expected that selecting for MFA would deliver greater gains than selecting for density. The reason that this doesn't occur appears to be due to the relative size of the genetic variation for MFA and density. Variances are shown in Table 6.3 and, using these variances, the additive genetic standard deviations for density and MFA are calculated to be 21 kg m^{-3} and 0.8 degrees respectively. Assuming genetic selection results in a two standard deviation shift in these traits, then the expected change in stiffness due to density is 12 GPa whereas the change due to MFA is only 0.2 GPa. These predicted changes were calculated using the

empirical relationship between stiffness, density and MFA described by Evans and Ilic (2001) and given as equation 6.1.

Another issue to consider when selecting for stiffness is the very low genetic correlation between the MFA of juvenile and mature wood (Figure 6.2), which indicates juvenile and mature MFA are different traits. It may be expected that selecting for mature wood stiffness (say by removing small short clear samples from outer wood) will not result in good genetic gains in juvenile wood stiffness. This would be important if a breeding goal was to overcome the comparatively low stiffness of juvenile wood. However, data from this study indicates that selecting using juvenile or mature wood stiffness gives very similar results and therefore the differences between mature and juvenile MFA will not be a problem. This presumably occurs because density, which has high correlations at different ages (Figure 6.2), is the primary determinant for genetic gains in stiffness.

6.5 CONCLUSION

Wood stiffness is under high genetic control and the potential gains that can be made by breeding for this trait are expected to be economically important, especially if wood products are to be sold as high strength products. In this study stiffness was predicted from measurements of wood density and MFA, and although both these traits are under genetic control, density has the primary influence. This appears to be due to the comparatively low genetic variance of MFA relative to that of density.

Selections for high stiffness can be made indirectly by selecting for wood density. There are only small extra gains to be made by selecting directly for stiffness and these are not expected to have any significant impact on the distribution of structural timber grades. Selection based on wood chip and kraft pulp indices are predicted to have favourable outcomes in terms of wood stiffness, but selection based on growth rate alone is expected to cause a significant drop in stiffness.

CHAPTER 7

7. Selection Strategies for Genetic Improvement of Wood Density

7.1 INTRODUCTION

Wood density is recognised as being important to product value and profitability for many different end uses. Increassed density has been shown to be important to the profitability of kraft pulp production (Borralho *et al.* 1993, Greaves *et al.* 1997a). Wood density is also important for cold caustic soda pulp production, although it appears low density is desirable (Banham *et al.* 1995, Jones and Richardson 1999). The importance of basic density to solid wood and composite products has not been precisely defined. However, in a review of the traits thought to be important for appearance grade timber, structural timber, veneer, and medium density fibreboard, basic density was flagged as important to all (Raymond 2000).

Tree breeding programs require large numbers of basic density measurements, and these need to be taken using low cost and non-destructive techniques. Basic density is commonly assessed using a core taken near breast height, which has been shown to be highly correlated to whole tree values (Lausberg *et al.* 1995, Raymond and Muneri 2001, Chapter 2 of this thesis). Density has also been assessed using a Pilodyn, which is an instrument that drives a flat-nosed pin into a wood sample with a fixed force. The depth of penetration is negatively correlated with basic density (Greaves *et al.* 1996, Raymond and MacDonald 1998, Raymond *et al.* 1998). Some studies have found Pilodyn precision to be low and unreliable for selecting individual trees (Raymond *et al.* 1998), although the low cost and simplicity of this method remain strong advantages and, for this reason, it is still being used.

This study had three aims. These were; firstly, to measure genetic parameters (heritabilities and genetic correlations) for basic density of a core and Pilodyn penetration over three sites. Secondly, to determine if differences occur between summer and winter Pilodyn assessments (i.e. shooting into early-wood or late-wood) in the accuracy of selection. And thirdly, to determine genetic gains under different sampling strategies involving diameter and basic density assessed using cores, Pilodyn, and combinations of both.

7.2 MATERIALS AND METHODS

7.2.1 Trial establishment and assessment

The genetic material used was open pollinated progeny from 40 native forest families from Toorongo Plateau in the central highlands of Victoria. Progeny trials were established in 1984 on three sites in northern Tasmania, all with good soil fertility and good productivity (Table 7.1). Stocking at planting was 1111 trees ha^{-1} (3 m by 3 m spacing) and survival at age 12 years was 81%. The trial design was a randomised complete block with single tree plots and 16 replications per site. Fifteen of the 40 families were only planted at two sites. The missing families were spread, in different combinations, across all sites and so every site had at least 35 families.

Table 7.1. Location and description of trial sites.

	Dial	Gog	Kamona
Latitude (South)	41° 10'	41° 29'	41° 08'
Longitude (East)	146° 04'	146° 23'	147° 40'
Altitude (m)	100	300	160
Rainfall (mm per year)	1060	1200	1150
Mean maximum temp. warmest month (°C)	22.3	21.8	23.4
Mean minimum temp. coolest month (°C)	3.8	2.4	2.5
Site index (m) [i]	26.3	27.5	28.6
Parent material	mudstone	basalt	granite

[i] Site index is mean dominant height at 15 years predicted using Farm Forestry Toolbox (Private Forests Tasmania 2001) after measuring the mean dominant height on each trial site.

All trees were measured for diameter at breast height (1.3 m) at age 12 years. Basic density was also measured at 12 years using a 12 mm diameter bark to bark core at a height of 0.9 m. Core sampling at this height has been shown to be a reliable predictor of whole tree values of basic density (Raymond and Muneri 2001, Chapter 2 of this thesis). Basic density was defined as oven-dry wood mass per unit volume of green wood, and was measured using the water displacement method (Hendrichs and Larson 1970; TAPPI 1989). Between 5 and 13 trees per family per site were randomly sampled (average of 8). Following an initial analysis, 11 trees were excluded due to high residuals (greater than 3 standard deviations from mean). These trees had low diameters, very little diameter increment between 6 and 12 years, and very high density. The number of trees and range of values are shown in Table 7.2.

Table 7.2. Description of data.

Trait		Min.	Mean	Max.	SD	n
D	Diameter, age 12 (cm)	10.1	21.1	40.4	6.0	1160
BD	Core basic density, (kg m^{-3})	362	451	568	31	841
PD_S	Pilodyn penetration, summer (mm)	7.0	12.2	17.0	1.6	853
PD_W	Pilodyn penetration, winter (mm)	6.0	11.4	16.5	1.7	607

Pilodyn penetration was measured on two occasions. The first measurement was done in late February (late summer) at age 13.5 years and the second was near the end of August (late winter) at age 14 years. Measurements were taken at a height of 1.3 m and, at each sampling time, two readings were taken per tree from a single bark window. Measurements were taken on opposite sides of the tree for summer and winter samples. Sampling in this way has been found to give accurate results, and opposite cardinal aspects have high repeatability (Greaves *et al.* 1996, Raymond and MacDonald 1998). Pilodyn penetration was measured on all trees assessed for basic density, but for the winter measurement only two sites (Dial and Gog) were assessed. The number of trees and range of values are shown in Table 7.2.

Trees less than 10 cm diameter were excluded from diameter and wood property assessments. Trees of this size were all strongly suppressed with no diameter increment between ages 6 and 12, and had atypical wood properties. These trees were found to inflate error variances.

7.2.2 Estimation of genetic parameters

The traits analysed were stem diameter (D), basic density (BD), Pilodyn penetration summer (PD_s) and Pilodyn penetration winter (PD_w). Variances, covariances, correlations and errors for each site and each trait were estimated simultaneously by fitting multi-variate multi-site models. Multi-variate analyses use information more efficiently and can improve the precision of genetic parameters when selected subsets of data are used (Dieters *et al.* 1999). Multi-variate multi-site models allow all genetic correlations to be calculated directly, and use appropriate variance-covariance matrices for each site. These models treat measurements on different sites as different traits. Analyses were done using ASREML (Gilmour *et al.* 1999), and the model fitted was:

$$Y = \mu + SITE + REP + FAM(SITE) + \varepsilon \quad (7.1)$$

where Y is a vector of data for each trait; μ is a vector of means for each trait; SITE are site effects for each trait fitted as a fixed factor; REP are within site replicate effects for each trait fitted as a fixed factor; FAM(SITE) are within site family effects for each trait fitted as a random factor; and ε is a vector of residuals

for each trait. Full inter-trait and inter-site variance and covariance matrices were fitted for the family and residual effects.

A second model was fitted (also for D, BD, PD_s and PD_w) to determine the importance of genotype by environment interactions and to estimate genetic correlations and heritabilities when data was pooled across sites. Error variances for each trait were all similar and therefore adjusting to a constant error variance was not considered necessary. This analysis was also done using ASREML and the model fitted was:

$$Y = \mu + SITE + REP + FAM + FAM.SITE + \varepsilon \quad (7.2)$$

where Y, μ, SITE, REP and ε are as previously defined; FAM are across site family effects for each trait fitted as a random factor; and FAM.SITE are site by family interaction effects for each trait fitted as a random factor. The model term FAM included an inter-trait variance and covariance matrix pooled across sites.

Heritabilities (narrow sense) and their standard errors were calculated by ASREML. Heritabilities for the individual site and multisite analyses were calculated as shown in models 7.3 and 7.4 respectively.

$$h^2 = \sigma^2_f / r\,(\sigma^2_f + \sigma^2_e) \quad (7.3)$$

$$h^2 = \sigma^2_f / r\,(\sigma^2_f + \sigma^2_{f.s} + \sigma^2_e) \quad (7.4)$$

Where h^2 is narrow sense heritability; σ^2_f, $\sigma^2_{f.s}$ and σ^2_e are, respectively, variance components for FAM, FAM.SITE and ε estimated in models 7.1 and 7.2; and r is the coefficient of relationship. The coefficient of relationship used was 0.4 which assumes a selfing rate of approximately 30% (Griffin and Cotterill 1988).

7.2.3 Evaluation of sampling strategies

Sampling strategies for basic density were evaluated by comparing genetic gains from different strategies. Four broad sampling strategies were evaluated and, within these, different sampling intensities tested (see Table 7.7). The sampling strategies were:

1. Random basic density samples from a set number of trees per family. The number of samples per family was either 6 or 12 and samples were taken using cores and Pilodyn.
2. Two-stage sampling using cores. In stage-1, random basic density samples were taken using cores from a set number of trees per family (either 6 or 12 cores per family). In stage-2, cores were taken from the top ranked trees on an index combining diameter and family basic density (either the top 10% or 20% of trees).
3. Two-stage sampling using Pilodyn and cores. In stage-1, random within-family Pilodyn measurements were taken from a set number of trees per

family (either 6 or 12). In stage-2, cores were taken from the top ranked trees as described in strategy 2.

4. Two-stage sampling using Pilodyn only. In stage-1, random within-family Pilodyn measurements were taken (either 6 or 12 measurements per family). In stage-2, Pilodyn measurements were taken from the top ranked trees on an index combining diameter and family Pilodyn data (either the top 10% or 20% of trees).

The data used to evaluate sampling strategies was diameter, core basic density and summer Pilodyn penetration (see Table 7.2). Trees for which no basic density measurements had been taken were excluded from this part of the analysis. This allowed gain to be calculated after 100% sampling for basic density, which was the benchmark used to compare all other sampling strategies. New data sets were created for each strategy using appropriate subsets of data.

Gains were estimated after calculating individual tree breeding values for diameter and basic density. Breeding values were calculated by fitting the following individual multivariate model using ASREML:

$$Y = \mu + SITE + REP + TREE + FAM.SITE + \varepsilon \quad (7.5)$$

Where Y is a vector of the data for the traits appropriate to each sampling strategy (combinations of D, BD, PD_s); μ, SITE, REP, FAM.SITE and ε are as previously defined; and TREE are individual tree breeding values for each trait. The model terms TREE and ε included an inter-trait variance and covariance matrix pooled across sites. These were fixed to values calculated in model 7.2 for all breeding value calculations (see footnote on Table 7.7 for values). Therefore an assumption in this sampling simulation is that appropriate genetic parameters are known. Separate models were run for each sampling strategy.

Trees were ranked on a selection index and the top 30 trees selected (3.6% of trees). This was done for each selection strategy and the index used was:

$$I = BV_D \,.\, W_D / \sigma_D + BV_{BD} \,.\, W_{BD} / \sigma_{BD} \quad (7.6)$$

Where I is a unitless index value; BV_D, and BV_{BD} are, respectively, breeding values for diameter and core basic density calculated using model 7.5; σ_D and σ_{BD} are additive genetic standard deviations for these traits; and W_D and W_{BD} are economic weights. The weights describe the relative importance of a standard deviation unit of each trait and were W_D=1 and W_{BD}=1. These are weights that approximate economic weights given by Borralho *et al.* (1993) and Greaves *et al.* (1997a) when converted to standard deviation units. Each selection strategy had its own set of breeding values and these were used in the selection index. Genetic gains were calculated by averaging breeding values of the selected population and were expressed relative to gains that could be obtained using the maximum strategy, which was 100% core sampling.

Sampling costs were calculated for each strategy. Core sampling for basic density is assumed to cost AU$10.5 per tree, which includes field collection and laboratory processing. The cost of Pilodyn measurements is assumed to be AU$1.5 per tree. These costs are based on the times taken during this study.

7.3 RESULTS AND DISCUSSION

7.3.1 Site differences

There were statistically significant differences between sites for diameter, basic density and Pilodyn penetration (Table 7.3). Growth rates on all sites were good and total volumes were predicted to be 235, 226 and 268 m^3 ha^{-1} for Dial, Gog and Kamona respectively.[12] Basic density was similar at Dial and Kamona, but 5% higher at Gog. Similarly, Pilodyn penetration was 5% lower at Gog. Pilodyn penetration was significantly lower in winter when compared to summer but the magnitude of differences was not consistent across sites. At Dial, winter measurements were 3% lower but at Gog, winter measurements were 12% lower.

Table 7.3. Least square means (± standard error) for each site.

Trait		Dial	Gog	Kamona
D	cm	18.4 ± 1.0	20.8 ± 1.0	23.5 ± 1.1
BD	kg m^{-3}	441 ± 5	470 ± 5	449 ± 6
PD_s	mm	12.3 ± 0.3	11.7 ± 0.3	12.3 ± 0.3
PD_w	mm	11.9 ± 0.3	10.3 ± 0.3	

7.3.2 Genetic parameters

Heritabilities for diameter were moderate (0.39 in a combined site analysis) and differences between sites were not significant (Table 7.4). For basic density, heritabilities were high (0.55 in a combined site analysis) and estimates varied significantly across sites (0.47 to 0.96). One site (Gog) had a very high heritability due primarily to a substantially higher additive genetic variance. Heritabilities for Pilodyn penetration were also high (0.47 in a combined site analysis) but less variable across sites (0.47 to 0.59). For the Gog site, Pilodyn heritability was significantly less than that of basic density. Pilodyn heritabilities were not significantly different between summer and winter measurements.

There were strong adverse genetic correlations between diameter and basic density (Table 7.5). Values for individual sites ranged from –0.13 to –0.79, and in a pooled analysis the correlation was –0.55. Genetic correlations between

[12] Volumes were predicted using Farm Forestry Toolbox (Private Forests Tasmania 2001) from mean dominant height data and basal area data.

diameter and Pilodyn penetration were positive, and very similar in magnitude to those for diameter and basic density with values ranging between 0.56 to 0.82. Genetic correlations between Pilodyn penetration and basic density were strongly negative and differences between sites were significant. The range of values was –0.79 to –0.98, and in a pooled analysis the correlation was –0.90 (Table 7.5).

Table 7.4. Variance components and heritabilities (± standard error) for diameter at breast height, basic density, and Pilodyn penetration.

Trait	Site	σ^2 family	σ^2 family.site	σ^2 error	h^2
Diameter	Dial	4.29 ± 1.52		25.03 ± 1.83	0.37 ± 0.12
(cm)	Gog	5.97 ± 2.07		28.04 ± 2.17	0.44 ± 0.13
	Kamona	5.45 ± 2.24		38.70 ± 3.12	0.31 ± 0.12
	All sites	5.58 ± 1.55	0	29.88 ± 1.29	0.39 ± 0.09
Basic density	Dial	168 ± 60		720 ± 64	0.47 ± 0.15
(kg m^{-3})	Gog	377 ± 111		605 ± 55	0.96 ± 0.19
	Kamona	201 ± 72		590 ± 59	0.64 ± 0.18
	All sites	202 ± 59	59 ± 26	689 ± 37	0.55 ± 0.13
Pilodyn,	Dial	0.47 ± 0.17		2.04 ± 0.18	0.47 ± 0.15
summer (mm)	Gog	0.48 ± 0.17		1.56 ± 0.14	0.59 ± 0.17
	Kamona	0.44 ± 0.16		1.58 ± 0.16	0.54 ± 0.17
	All sites	0.43 ± 0.12	0	1.86 ± 0.10	0.47 ± 0.11
Pilodyn,	Dial	0.58 ± 0.21		2.51 ± 0.22	0.47 ± 0.15
winter (mm)	Gog	0.35 ± 0.13		1.63 ± 0.15	0.44 ± 0.14
	All sites	0.44 ± 0.13	0	2.14 ± 0.13	0.42 ± 0.11

Table 7.5. Genetic correlations (r_G) with standard errors above diagonal and phenotypic correlations (r) below diagonal.

Site		D	BD	PD_S	PD_W
Dial	D		-0.13 ± 0.25	0.56 ± 0.20	0.60 ± 0.21
	BD	-0.17 *		-0.79 ± 0.13	-0.71 ± 0.14
	PD_S	0.12	-0.45 *		0.98 ± 0.05
	PD_W	-0.04	-0.45 *	0.70 *	
Gog	D		-0.79 ± 0.12	0.68 ± 0.17	0.51 ± 0.23
	BD	-0.12		-0.98 ± 0.04	-0.95 ± 0.06
	PD_S	0.04	-0.64 *		0.98 ± 0.05
	PD_W	-0.12	-0.60 *	0.66 *	
Kamona	D		-0.72 ± 0.20	0.82 ± 0.19	
	BD	-0.03		-0.81 ± 0.11	
	PD_S	0.07	-0.58 *		
All sites	D		-0.55 ± 0.15	0.63 ± 0.14	0.52 ± 0.16
	BD	-0.11		-0.90 ± 0.06	-0.87 ± 0.07
	PD_S	0.03	-0.53 *		0.96 ± 0.03
	PD_W	-0.08	-0.54 *	0.68 *	

* Significantly different from 0 at 0.05.

There were no significant genotype by environment interactions for diameter or for Pilodyn penetration in either summer or winter. For these traits, family by site

variance was zero (Table 7.4) and genetic correlations between sites were high (Table 7.6). Genotype by environment interaction for basic density was significant but relatively small, with family by site variance accounting for 6% of the total variation (Table 7.4), and between site genetic correlations ranging from 0.68 to 0.89 (Table 7.6). The interaction appeared to be caused by minor rank changes from many families and excluding groups of families did not substantially reduce the interaction.

Table 7.6. Genetic correlations (± standard error) between sites.

Trait	Dial & Gog	Dial & Kamona	Gog & Kamona
D	1.09 ± 0.10	0.95 ± 0.15	1.15 ± 0.12
BD	0.76 ± 0.14	0.68 ± 0.19	0.89 ± 0.11
PD_s	0.76 ± 0.17	0.99 ± 0.13	0.88 ± 0.14
PD_w	0.99 ± 0.13		

Genetic parameters for *E. nitens* basic density and Pilodyn penetration have been published by Greaves *et al.* 1996, Gea *et al.* 1997, and Tibbits and Hodge 1998. Heritabilities for basic density (combined site analyses) range from 0.45 to 0.73 and the value from this study falls within the middle of that range. Similarly, the heritability for Pilodyn penetration from this study falls within the published range, which is 0.41 to 0.60. Genetic correlations between basic density and Pilodyn have always been found to be high (–0.92 to –1) and this study was no exception (–0.90). However, genetic correlations for diameter-basic density and diameter-Pilodyn calculated in this study are very different to those found elsewhere. Diameter-Pilodyn correlations have been reported as being near zero (Gea *et al.* 1997, Tibbits and Hodge 1998) but in this study they were strongly adverse (0.63). The same authors report diameter-basic density correlations from zero to weakly negative (–0.24), but in this study the correlation was found to be strongly negative (–0.55).

7.3.3 Comparing gains with different sampling strategies

Predicted genetic gains were calculated using index selection with equal emphasis placed on tree diameter and density. Under the most intensive sampling strategy (sampling approximately 24 trees per family and 40 families) basic density was predicted to increase by 26 kg m^{-3}. This represents an increase in the mean value of nearly 6% (from 451 to 477 kg m^{-3}). The cost of this sampling strategy is estimated to be AUD$10 K. A range of alternate basic density sampling strategies was evaluated and the gains and costs are shown in Table 7.7. The gains have been expressed as a percentage of this value (i.e. 100% is a gain of 26 kg m^{-3}).

A two-stage core sampling strategy can deliver at least 74% of potential gains at a much lower cost (strategy 2 in Table 7.7). This strategy involves randomly sampling all families, making initial selections using individual tree diameter and

family mean basic density, and then re-sampling highly ranked trees. Differences between sampling the top 10% and top 20% are not large; 13% of the total potential gain (or about 3 kg m^{-3}) is foregone by taking a smaller 'top' sample. Increasing the size of the random sample within families from 6 to 12 did not substantially increase gains. Therefore an efficient use of a limited sampling budget would be to sample fewer trees per family in stage-1 (6 trees appears adequate) and more 'top' trees in stage-2.

Table 7.7. Comparison of genetic gains in basic density and costs (x AU$1000) for different sampling strategies. Data is expressed as the percentage of gain obtained relative to sampling all trees using cores.

Sampling strategy		Samples per family 12		6	
1	**Random within family sample** [i]				
1.1	Cores	56%	($5.0)	33%	($2.5)
1.2	Pilodyn	22%	($0.7)	9%	($0.4)
2	**Two-stage, cores + cores** [i]				
2.1	Family cores + cores top 10% D-BD index	76%	($6.0)	74%	($3.5)
2.2	Family cores + cores top 20% D-BD index	89%	($7.0)	87%	($4.5)
3	**Two-stage, Pilodyn + cores** [i]				
3.1	Family Pilodyn + cores top 10% D-BD index	65%	($1.7)	39%	($1.4)
3.2	Family Pilodyn + cores top 20% D-BD index	70%	($2.7)	57%	($2.4)
4	**Two-stage, Pilodyn + Pilodyn** [i]				
4.1	Family Pilodyn + Pilodyn top 10% D-PD index	20%	($0.9)	12%	($0.5)
4.2	Family Pilodyn + Pilodyn top 20% D-PD index	29%	($1.0)	16%	($0.6)

[i] Trees selected on an index combining diameter and basic density with equal weighting per standard deviation unit on each trait.

A two-stage sampling strategy involving diameter and Pilodyn for the stage-1 family sample and cores for the stage-2 individual tree sample also gave reasonable gains provided the family sample was sufficiently large (strategy 3 Table 7.7). Up to 70% of potential gains can be achieved under this sampling strategy. This strategy costs about half that of a two-stage coring strategy and would be suitable if the sampling budget is limited. However, gains were considerably less with only 6 Pilodyn readings per family which suggests that this number of Pilodyn readings does not reliably rank families.

Sampling using a diameter and Pilodyn alone delivered substantially less gain (strategy 4 Table 7.7). At best, only 29% of potential gains were achieved. Pilodyn readings cannot accurately rank an individual tree for basic density and sampling more 'top' trees using a Pilodyn gave only a marginal increase in gains. If the sampling budget is limited then a stage-1 Pilodyn sampling and stage-2 core sampling will always give substantially better gains for virtually the same expenditure.

Figure 7.1. Scatter plot of individual tree breeding values for basic density and Pilodyn penetration.

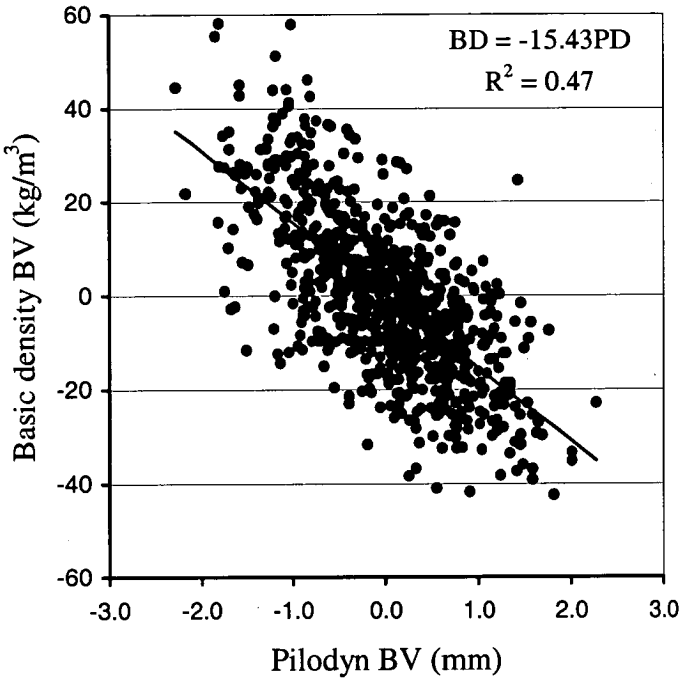
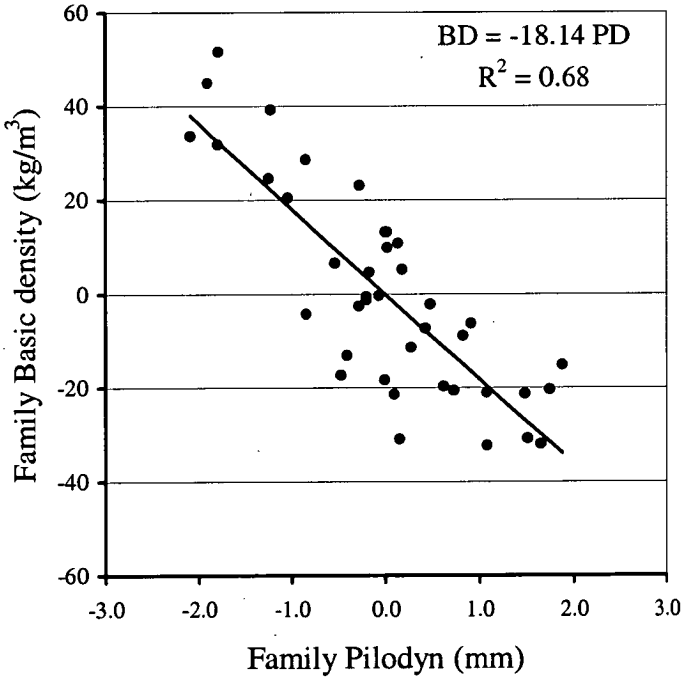


Figure 7.2. Scatter plot of family BLUPs for basic density and Pilodyn penetration. Values shown are based on 12 samples per family.



The reasons for low gains when using Pilodyn sampling strategies are illustrated in Figure 7.1. Although basic density and Pilodyn penetration are well correlated, there are wide ranges of density values for any given Pilodyn reading. When doing forward selections (that is selecting progeny) as was done in the strategies tested here, this high variation impacts on gains. The impact is made more severe when selecting multiple traits (in this case Pilodyn and diameter) because trees with lower Pilodyn readings are selected in order to obtain acceptable values in the other trait. Figure 7.1 shows that variation is greater for values close to the mean. If the selection strategy was for backward selections (that is selecting families or parents) then Pilodyn may be an acceptable sampling method. This is illustrated in Figure 7.2. Although there is still reasonably large variation in basic density for any given Pilodyn reading, the magnitude of that variation for family values is about half that of progeny values. This simply reflects the 'safety in large sample numbers' implicit in backward selections.

Differences in genetic gains for summer and winter Pilodyn assessments were compared for the two-stage Pilodyn plus cores sampling procedure (i.e. strategies 3.1 and 3.2). It was thought that shooting a Pilodyn into a band of late-wood may give different results than when shooting into a band of early-wood. Gains were almost identical and therefore Pilodyn assessments in different seasons do not appear to alter the discriminating power of measurements.

In the strategies described above the second stage sample (i.e. the top 10 or 20% of trees) was selected using both the individual tree diameter data and family basic density data. A second stage sample is sometimes selected using diameter data only, the assumption being that selected trees will only come from trees with very good growth rates. However, in this study, at least 20% of potential gain in basic density (or 5 kg m^{-3}) was foregone when selecting the stage-2 sample using diameter data only (Table 7.8). This reflects the strongly negative genetic correlation between diameter and basic density, and selected trees are not necessarily limited to those with large breeding values for diameter.

Table 7.8. Comparison of genetic gains in basic density using different stage-2 sampling procedures. Data is expressed as the percentage of gain obtained relative to sampling all trees using cores.

Sampling strategy		Stage-2 selection method	
		D only	D-BD index
2	**Two-stage, cores + cores**		
2.1	Family cores (12 per family) + cores top 10%	56%	76%
2.2	Family cores (12 per family) + cores top 20%	59%	89%
3	**Two-stage, Pilodyn + cores**		
3.1	Family Pilodyn (12 per family) + cores top 10%	36%	65%
3.2	Family Pilodyn (12 per family) + cores top 20%	38%	70%

7.4 CONCLUSION

Heritabilities for basic density and Pilodyn penetration were high and the two traits were highly correlated at the genetic level. However, for both traits there were strong and adverse genetic correlations with stem diameter. Heritabilities and genetic correlations for Pilodyn assessed in summer (shooting into early-wood) and winter (shooting into late-wood) were not significantly different.

Genetic gains are highest using index selection based on diameter and density assessed from core samples. An efficient two-stage core sampling strategy is to sample relatively low numbers per family (as few as 6 individuals) in stage-1 and sample up to 20% of the top trees ranked on a diameter-basic density index in stage-2. This strategy delivered 87% of the gains possible by core sampling all trees. A two-stage sampling strategy using Pilodyn to assess random individuals from each family and cores to assess selected individuals can deliver up to 70% of gains at a much lower cost. If using this strategy larger numbers of individuals per family need to be sampled in stage-1 (12 was substantially better than 6 in this study). Selecting for basic density using an index combining diameter and Pilodyn alone is not recommended despite the very high genetic correlations between basic density and Pilodyn. Pilodyn alone delivered no more than 29% of potential gains, even when large samples were taken.

CHAPTER 8

8. Conclusions

8.1 BREEDING FOR IMPROVED WOOD QUALITY

There is significant genetic variation in the wood properties of *E. nitens* and tree breeding can potentially deliver significant improvements in the quality of wood used for pulp and paper products, appearance grade timber, and structural grade timber. Each of these product grouping requires different wood properties, and the major findings with regard to each of these groups are as follows:

Pulp and paper

The most important wood properties for kraft pulp production are wood density and pulp yield. Wood density, which was predicted using cores taken near breast height, and pulp yield, which was predicted using cellulose content of wood cores, were found to be under strong genetic control. Wood consumption, which is a measure of the amount of wood required to make one tonne of kraft pulp, was predicted to decrease by approximately 3% after selecting for these traits on a combined index (a decrease is favourable for wood consumption). When selecting for appearance and structural grade products, the gains in wood consumption are very similar due to the selection for wood density and favourable correlations between growth rate and pulp yield.

A sound understanding of how breeding for improved wood density influences paper quality is a gap in current knowledge. There is a risk that an increase in wood density, whilst improving the profitability of pulp production, may adversely affect some paper properties. For example, high density wood may have thick fibres and result in a decrease in paper of lower strength. Therefore there is a need to extend work on breeding objectives from the production of pulp to the production of paper.

Appearance grade products

Checking is a major cause of degrade in appearance products and is known to be strongly influenced by collapse. Collapse is a trait that is under moderate to high genetic control. The percentage of product in different appearance grade categories is predicted to change substantially with genetic selection. If selecting for diameter alone, a large increase in checking is predicted and very few boards

are expected to be acceptable for the joinery market. Selection based on wood chip or kraft pulp indices is expected to cause minimal changes in checking and therefore this is a reasonable option if current wood quality is acceptable for the appearance grade market. If it is required to lower the incidence of checking, then an index including diameter and collapse is recommended. Selecting in this way is predicted to improve growth and decrease the incidence of checking to a point where most boards will be suitable for the joinery market.

Wood decay is another potential cause of degrade in appearance products and represents a serious risk when using silvicultural regimes that involve pruning or thinning. The incidences of wound-rot and of heart-rot are both under strong genetic control; however, wound-rot will probably be the trait that will be most relevant to improving the value of *E. nitens* sawlog plantations. For multi-trait selection, large gains in this trait do not appear possible and an appropriate selection strategy may be to ensure the incidence of decay becomes no worse than it is in the current population. This appears achievable without sacrificing large gains in other traits. Good gains appear possible when selecting for decay resistance alone though gains in other traits are forgone. This strategy may be appropriate if selecting a deployment population for sites highly susceptible to decay.

Structural products

Wood stiffness is the major determinant of timber structural grades. It is under high genetic control and the potential gains that can be made by breeding for this trait are expected to be economically important, especially if wood products are to be sold as high strength products. In this study, stiffness was predicted from measurements of wood density and MFA, and although both these traits are under genetic control, density has the primary influence. This appears to be due to the comparatively low genetic variance of MFA relative to that of density. Therefore selections for high stiffness can be made indirectly by selecting for wood density. There are only small extra gains to be made by selecting directly for stiffness and these are not expected to have any significant impact on the distribution of structural timber grades. Selection based on wood chip and kraft pulp indices are predicted to have favourable outcomes in terms of wood stiffness, but selection based on growth rate alone is expected to cause a significant drop in stiffness.

8.2 WOOD DENSITY SELECTION STRATEGIES

Wood density is a fundamental trait to all product groupings. It is not practical to sample every tree for wood properties and therefore the best sampling strategy needs to be determined. An efficient two-stage sampling strategy is to use bark to bark wood cores to sample relatively low numbers per family (as few as 6

individuals) in stage-1 and sample up to 20% of the top trees ranked on a diameter-basic density index in stage-2. This strategy delivered 87% of the gains possible by core sampling all trees. A two-stage sampling strategy using Pilodyn to assess random individuals from each family and cores to assess selected individuals can deliver up to 70% of gains at a much lower cost. If using this strategy, larger numbers of individuals per family need to be sampled in stage-1 (12 was substantially better than 6 in this study). Selecting for basic density using an index combining diameter and Pilodyn alone is not recommended despite the very high genetic correlations between basic density and Pilodyn. Pilodyn alone delivered no more than 29% of potential gains, even when large samples were taken.

8.3 CORRELATION BETWEEN PRODUCT GROUPS

Plantations used to grow solid wood products are expected to produce wood suitable for different purposes. A selection strategy that increases the value for one market but results in the crop being less suitable for other markets will probably be considered risky, especially where there is uncertainty about future markets. Therefore there is a need to know how the quality of one product group changes when selecting for another.

Predicted changes in the quality of pulpwood, appearance grade timber and structural grade timber under different selection strategies are summarised in Table 8.1. Selecting for growth alone results in a substantial decline in wood quality for all product groupings and an increase in the amount of wood required to produce a tonne of pulp. Consequently, this is not a sound strategy if high quality products are to be produced. Improvements in the quality of pulpwood are obtained when selecting for both appearance and structural products and therefore pulpwood breeding goals appear compatible with those for solid wood products. Gains in the quality of structural products are reasonable with any strategy that includes wood density and therefore this strategy is also reasonably compatible with other breeding goals. Substantial gains in the quality of appearance grade products are not achieved unless selections are made for collapse, although small gains are made in appearance product quality under other strategies.

Therefore it appears that breeding objectives for different wood products are generally compatible and no strategy (apart from selecting for growth alone) will cause the quality of any product group to decline. However, greater genetic gains for some specific traits are possible (such as collapse and decay resistance) and a key decision will be to select a product group in which the maximum gains should be sought.

Table 8.1. A summary of the improvements in pulpwood, appearance grade timber and structural grade timber under different selection strategies.

Selection strategy	Product grouping		
	Pulp	Appearance	Structural
	Wood consumption (m^3/t pulp) [i]	% select grade or better [i]	% F14 or better (>12 GPa) [i]
Current population	3.77	65%	43%
Growth	3.81	8%	36%
Growth + wood density	3.66	75%	52%
Kraft pulp	3.66	68%	49%
Appearance sawlog	3.68	93%	43%
Structural sawlog	3.66	75%	56%

[i] This data is based upon the five selection strategies and gain predictions in Chapters 3, 4 and 6 (see Tables 3.7, 4.11 and 6.8).

8.4 FUTURE DIRECTIONS

The Australian hardwood forest industries are currently moving from native eucalypt forests which are characterised by long rotations and relatively slow growth rates, to plantation eucalypt forests which are characterised by much shorter rotations and faster growth rates. The plantation eucalypt resource was originally developed to supply pulpwood and genetic, silvicultural and site selection strategies were successfully developed to meet that product requirement. The challenge for the industry is now to develop genetic, silvicultural and site selection strategies capable of meeting the requirements of solid wood markets. Each of these management tools has their advantages and disadvantages and a forest manager needs a detailed knowledge of how wood quality is affected by each of these tools.

Site type is known to have a strong influence on many wood properties, but the reality for most forest growers is that they have a limited ability to alter their forest estate. However, opportunities may exist to develop breeds that are targeted for specific sites. For example, there may be opportunities to make selections which seek to overcome some major site limitation such as a high incidence of decay, or a high tendency for collapse and checking. This may be a viable strategy for high value products (such as appearance products on highly productive sites) but is unlikely to be viable for low value products (such as pulpwood), especially if significant trade-offs need to be made in growth rate. It would also require a detailed knowledge of the wood properties across different sites types and, currently, this knowledge is limited.

Silvicultural management appears the best way to influence the morphological properties of a log such as piece size, knot characteristics, and log sweep. This is done through the manipulation of thinning, pruning and stocking (e.g. Neilsen and

Pinkard 2000). The limited application of genetics for these traits reflects the low genetic control of branching (see Chapter 5) and straightness.[13] Silvicultural management can also minimise the risk of decay (e.g. Wardlaw and Neilsen 1999) and it may also be a means of minimising the effects of growth stresses which are implicated in log end splitting and deformation of boards during sawing (e.g. Maree and Malan 2000). Knowledge of how silvicultural management influences the wood quality of temperate eucalypts for solid wood products is limited, but experience in other regions (e.g. South Africa, see Maree and Malan 2000) suggests that its influence will be small.

Genetic improvement programs are likely to be the most important tool for improving some of the fundamental wood properties that define both suitability and value for different product groupings. For pulp and paper products, genetic selection can make important improvements to the profitability of pulp production. However, future work needs to develop a better understanding of how to breed for fibre properties as they relate to paper making. For appearance products, a key goal is to produce timber free of defects such as checking, collapse, and decay. This thesis has found that genetic selection can have important influences on these properties, but work needs to be extended to evaluate the relationships between selection traits and objective traits. For structural products, a goal is to produce timber with high stiffness. It appears that genetic selection can be used to achieve this goal but, as for appearance products, there is a need to evaluate the relationships between selection traits and objective traits. There is also a need to look more closely at the ability to breed to reduce the large variation between juvenile wood stiffness and mature wood stiffness, which would achieve greater product uniformity. For all product groupings there is a need for precise knowledge of economic weights for each product group. This is difficult at present for a number of reasons, such as poorly defined markets, a young and small plantation timber industry (in Australia), an industry which does not give strong market signals to wood growers, and the likelihood that changing milling technology will alter economic values. Nevertheless, this work should not be delayed because decisions do need to be made now.

A goal for the Australian forest industries should be to rapidly move forward in the domestication of eucalypts in general and *E. nitens* in particular. This is an essential part in making the transition from a native forest resource to a plantation resource. Tree breeding will be an essential part of this process, and selection for wood properties will be integral to future tree breeding strategies. The immediate need is to develop a breed with functionality across a broad range of product

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[13] Stem straightness data was collected from the trials used in this current study, but was not reported in this thesis. The heritability was not significantly different from zero.

groups and the studies done as part of this thesis suggests this is achievable. In the longer term and as the industry matures it is possible that there will be breeds and clones developed specifically to match product, site and silvicultural requirements. Such strategies will fully capitalise on the inherently high heritabilities for wood properties, and the large selection differentials possible with tree breeding.

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